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Space and Prey Use by Northern Pike (*Esox lucius* L.) in Two Alberta Lakes

by

©

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A THESIS
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ABSTRACT

Factors affecting the distribution and foraging rate of northern pike were assessed in two small deep, north temperate lakes. The major factors evaluated were a size-related trophic shift and a seasonal or monthly trophic shift. The effects of temperature and oxygen concentration gradients and aquatic macrophyte distribution on these niche dimensions were also examined.

The relationships between spatial and temporal resource use and a seasonal trophic shift in northern pike were examined in Mere Lake, Alberta, where the adult component of the pike population exhibited a marked dietary change in the latter part of the summer. The spatial and temporal partitioning of resources between two distinct trophic classes of northern pike (young-of-the-year and adults) was examined in Roi Lake, Alberta. Studies were conducted during the summer months of 1982 (Roi Lake) and 1983 (Mere Lake) using a variety of live-capture techniques, underwater observation, and standard limnological measurements.

To assess changes in distribution and activity, transect lines (50 to 200 metres in length) were laid down in representative habitat categories. Three metre wide strips along each transect were surveyed using snorkel and SCUBA to determine the size, microhabitat, and activity status of all pike observed. Distribution and activity of northern pike were assessed during the daylight hours and on a month to month basis in Roi Lake. In Mere Lake, distribution patterns were determined on a monthly basis.

Several parameters of the underwater census technique were evaluated. These include: independence of samples, reaction of northern pike to observer presence, and the consistency of the depth distribution of pike. Samples were 92 percent independent, the reaction of the pike to diver presence contributed approximately 4 percent error to transect census results, and the depth distribution of pike was constant throughout the summer months.

Northern pike were observed approximately 662 times on transects in Roi Lake. There was little temporal variation in the activity or in the distribution of the pike in this population during the daylight hours of the summer months. However, juvenile and adult pike differed in microhabitat selection and dispersion pattern.

Rank analysis indicated no correlation between the distribution of young-of-the-year pike in Roi Lake and the distribution of their dominant prey item, the Iowa darter (Etheostoma exile). Differences were observed between the habitat use of adult pike and their major prey item, the dragonfly nymph (S.O. Anisoptera). Activity in both juvenile and adult pike was primarily confined to the daylight hours. Activity, as recorded by direct observation underwater did not adequately reflect rates of foraging activity; however, there was indirect evidence of a relationship between foraging rate and prey type.

In Mere Lake, observations were limited to the adult segment of the population (pike age 1 year or older). A total of 237 observations were recorded for pike on the transects in Mere Lake. Again, pike showed little variation in depth distribution and microhabitat use during the summer months. Theyselected areas of shallow water (<1.0 m in depth) characterized by the presence of emergent vegetation.

Pike fed primarily on dragonfly nymphs (S.O. Anisoptera) and freshwater shrimp (O. Amphipoda) during May, June, and July in Mere Lake but showed a marked dietary shift in August. This was characterized by a decrease in the frequency of occurrence of the dominant invertebrates and a significant increase in the frequency of occurrence of perch in the diet.

Overlap was observed in the depth distribution of northern pike and the major invertebrate taxa they consumed in Mere Lake. Both predator and prey exhibited a predominantly littoral distribution. Overlap in the depth distribution of pike and perch was low in June and July but relatively high in August. This was attributed to a seasonal movement of perch into the shallow littoral areas of the lake.

The foraging rate of adult pike in Mere Lake decreased in August as their diet changed to include a significantly higher proportion of fish. Evidence for this decrease was: a high percentage of empty stomachs in August, a significant decrease in the number of food items in the stomach of each fish, and a corresponding increase in mean prey size.

There was evidence to suggest that water temperature, dissolved oxygen concentration, and the presence of vegetation influenced the depth distribution of the northern pike in both populations. Within the selected depth stratum, ecological

interactions appear to have been responsible for the finer resolution of microhabitat use, intraspecific predation pressure in the case of the juveniles, and foraging strategies in the case of the adult pike.

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GENERAL INTRODUCTION

Many temperate freshwater fishes are viewed as being plastic with respect to habitat use and foraging strategies. Evidence to support this idea is generally derived from the wide range of prey species found in their stomachs and the diurnal and seasonal changes in habitat use exhibited by a number of temperate fish species. North temperate lakes are highly variable throughout the year with respect to biotic factors (abundance of various prey species, conspecifics, etc.) and abiotic factors (temperature, oxygen concentration, water level) (Emery 1973 1978, Keast 1978, Helfman 1979). This dynamic aspect of the temperate lake environment may demand the ecological adaptability of fish species to different physical and biotic conditions (Emery 1978, Partridge 1978, Helfman 1979). The ability of predators which live in these lakes to use different habitats in response to fluctuating prey abundance or to change diet to take advantage of seasonally abundant prey species may be important in determining survival and reproductive success.

The indeterminate nature of fish growth conveys a high degree of plasticity to fish species; and development in fishes is often characterized by age- or size-related spatial, temporal, dietary, and social changes. Thus, age groups may occupy different ecological niches increasing the complexity of inter- and intraspecific relationships in fish communities (Keast 1970, Keast 1977, Werner et al. 1977, Helfman 1978).

Plasticity in foraging strategy is reflected in the seasonal or monthly trophic shifts exhibited by a number of temperate fish species including perch, bluegill, char, and bass (Frost 1954, Keast 1970, Keast 1977), size-related trophic shifts as observed in perch, bluegill, crappie, walleye, and pike (Frost 1946, Frost 1954, Keast 1970), and major geographic differences in diet. These trophic shifts characteristic of various temperate fish species may be limited to changes in the proportions of the kinds of foods consumed or may involve a major shift to a new prey type.

One would predict that these size-specific and seasonal trophic shifts would be related to shifts in habitat use and foraging rate, where foraging rate is defined as the intake of prey items per unit of time.

The northern pike (Esox lucius L.) is a top predator in many freshwater ecosystems of the north-temperate region. Pike are very plastic with respect to foraging strategies exhibiting age- and size-related trophic shifts (Hunt and Carbine 1950, Frost 1954, Munro 1957, Franklin and Smith 1963, Bregazzi and Kennedy 1980, Mann 1982), seasonal dietary shifts (Frost 1954, Lawler 1965, Mann 1982, Mackay unpubl. data), and major geographic differences in diet.

Numerous studies have attempted to relate dietary shifts in northern pike to the availability of prey species (Frost 1954, Lawler 1965, Christiansen 1976, Diana 1979a, Mann 1982); however, few workers have succeeded in clearly evaluating the distribution of both pike and their prey, changes in the availability of prey species, and the relationships between trophic shifts and the distribution pattern and foraging rate of the predator.

The present investigation was designed to assess the factors affecting the distribution and foraging rate of northern pike. The major factors evaluated were a size-related trophic shift, a seasonal or monthly trophic shift, and aquatic macrophyte distribution in addition to various abiotic factors. The major technique used in this study to obtain data concerning pike distribution and activity was the direct visual census of transects. Direct observation techniques have been widely used in the area of coral reef fish ecology (Bardach 1959, Luckhurst 1977, Leum and Choat 1980, Dubin 1981); and, although relatively new in studies of temperate fish species, visual census methods have been used to yield approximate counts of fish numbers, and information concerning habitat use, activity patterns, and feeding ecology in various temperate fish communities (Emery 1973, Keast and Harker 1977, Werner et al. 1977, Helfman 1979). However, there are numerous assumptions and constraints of the visual census technique which should be taken into account in the choice and design of experimental procedures. The first chapter of this thesis deals with the use of visual census techniques for studies of temperate freshwater fish.

This thesis addresses two major hypotheses: 1. seasonal (monthly) trophic shifts are associated with changes in the distribution patterns and foraging rates of northern pike and 2. size-related trophic shifts are associated with differential distribution patterns and foraging activities between trophic classes. In testing these hypotheses, field studies

were conducted on pike populations in two small, deep, north temperate lakes located in central Alberta. The spatial and temporal partitioning of resources between two distinct trophic classes of northern pike (young-of-the-year and adults) was examined in Roi Lake, Alberta during the summer months of 1982. The results of this study are presented in the second chapter. Relationships between spatial and temporal resource use and a seasonal dietary change in northern pike were examined in Mere Lake, Alberta, where the adult segment of the pike population (1 year or older) exhibited a marked trophic shift in the latter part of the summer. This study was conducted during 1983, and the results are reported in the third chapter. The research was conducted at Roi Lake (1982) and Mere Lake (1983) using a variety of live-capture techniques, underwater observation, and standard limnological measurements.

Initially, I planned to spend a part of the second field season reassessing the pike population in Roi Lake. This would have tested the temporal stability of the patterns observed in 1982 and the predictions developed from these data. Apparent disturbance of resident loons in the first field season precluded the possibility of subsequent data collection. I believe that the value of the research is not significantly reduced by a one-season analysis.

I. ESTIMATION OF FISH POPULATION SIZE USING VISUAL CENSUS

A. INTRODUCTION

A fundamental aspect of any population related investigation is an estimate of population size. The significance of this parameter has stimulated the development of a number of procedures, both direct and indirect to estimate either relative or absolute population size. The most appropriate procedure depends upon the objectives of the study, characteristics of the species being studied, as well as the time, resources, and personnel available.

As part of a research program investigating the distribution and activity of Esox lucius (northern pike) in a small, meromictic Alberta lake, an attempt was made to estimate the size of the resident population using a visual census technique. The method of estimating population size was designed to determine the number of pike age 1 year or older in Roi Lake. The young-of-the-year were not included in the estimate; as mortality is extremely high during the first 4 to 5 months of life, and numbers thus show marked fluctuations over time (Franklin and Smith 1963, Mann 1980). This report describes the technique used and the precision of the estimate obtained.

B. METHODS

Methods of Estimating Population Size: Strengths and Limitations

As the goal of the research was to study a number of behavioral aspects of the population, the use of standard population estimating techniques such as rotenone application or the reduction of catch per unit effort, which involve high induced mortality was not feasible.

Various mark-recapture techniques were suitable with respect to their non-destructive nature; however, validation of the general assumptions of these methods (random sampling, complete mixing of the population) was not possible. Due to the differential response to catching gear by different size categories within the resident population, it would have been difficult to capture a random sample of northern pike in Roi

Lake without the use of a number of complementary capture techniques. In addition, a tagging study designed to detect major distributional changes in the population of Roi Lake indicated that large-scale movements (>100 m) by individuals were limited during the summer months. Hence, the assumption of homogeneous dispersal of marked animals (complete mixing) within the entire lake between the time of release and the time of the subsequent recapture sample could not be justified.

In recent years, the swimming of transects by free divers has been used to obtain approximate counts of fish numbers in both tropical and temperate waters (Brock 1954, Bardach 1959, Northcote and Wilkie 1963, Keast and Harker 1977, Werner et al. 1977, Larson 1980, Leum and Choat 1980). The visual census technique provides a relatively rapid and efficient method of estimating population size without disturbing the fish assemblage by taking a physical sample (Northcote and Wilkie 1963, Sale and Douglas 1981).

There are, however, various assumptions and constraints involved in using the visual census technique which should be considered in the choice and design of the experimental procedures. The major constraint of this type of survey is its necessary confinement to reasonably clear water and moderate to shallow depths (<30 m). Thus, in many eutrophic lakes with characteristically low visibility this method is unsuitable. A major assumption of the visual census estimate is that the total number of fish observed constitutes a measure of the actual number present. The validity of this assumption depends upon various observational variables: crypticity of the fish (or the screening effect of the habitat), hiding or dispersion of alerted fish in front of divers, varying visibility of different size classes, duplicate counts, experience and speed of the observer, and conditions related to weather, turbidity, etc. In most cases, these problems are reflected in a conservative population estimate (Brock 1954, Northcote and Wilkie 1963, Hirst 1969, Emlen 1971, Keast and Harker 1977).

Constraints of the visual census technique may be overcome by selecting a suitable study site; and certain observational difficulties may be alleviated with appropriate methodology, or the error estimated by appropriate experimentation and analyses.

Attributes of Roi Lake and Northern Pike Relative to Visual Census Methodology

Various morphological and limnological attributes of Roi Lake justify the application of the visual census technique for the estimation of the size of the resident pike population. Roi Lake is a small, deep, meromictic lake located 40 kilometres northwest of Edmonton, Alberta (53°51'N,114°05'W). The lake has a surface area of 8 hectares, a manageable size for surveying since a large area can be sampled in proportion to the total area, and the sampling can be repeated. Roi Lake has a maximum depth of 21 metres and is characterized by a simple basin morphometry. The littoral zone was composed of a nearly continuous bench of the emergent macrophyte Scirpus extending as far as 20 metres from shore to a depth of 0.8 metres and a steep slope continuing to a depth of 5 metres dominated by the macroalga Chara (Figure 1.1). The littoral area was relatively homogeneous with respect to these vegetation characteristics. The lake was thermally stratified with the metalimnion commencing at a depth of 4 to 5 metres; and, characteristic of meromictic lakes, the hypolimnion (>8 m in depth) is permanently anoxic thus limiting the distribution of the resident fishes to depths of less than 8 metres. The unproductive nature of Roi Lake was reflected in good visibility; a mean Secchi disk reading of 6.4±1.2 metres (standard deviation, n=20, Appendix I, Table 1) was recorded during the period of investigation.

Certain ecological and behavioral features of northern pike also make them amenable to visual census techniques. Pike are inactive up to 80 percent of the time during the daylight hours of the summer months (Christiansen 1976, Diana 1980) and are typically located in the illuminated littoral zone of north temperate lakes (Diana et al. 1977, Chapman and Mackay 1984a and 1984b).

Population Estimate

As a preliminary survey of the distribution of northern pike (age 1 year or older), randomly selected areas of the lake were censused by snorkel and SCUBA (self-contained underwater breathing apparatus) in the first 2 weeks of June, 1982. Results of this survey indicated that 90 percent of the observed pike were associated with vegetation and in less than 1.5 metres of water.

From the point-of-view of mathematical description, the use of the entire lake as a discrete sampling unit (an unrestricted random sample) would be the easiest to deal with and would provide an unbiased estimate. However, the apparent depth selection exhibited by northern pike in the preliminary survey indicated considerable spatial variation ie. a zonation or a pattern of density. Thus, a stratified systematic regime was considered to be the appropriate sampling method.

The lake was divided into seven zones (Figure 1.1), 150 to 200 metres in length. End boundaries of the zones were demarcated on the shoreline with surveyor's tape and underwater, using bricks tagged with fluorescent tape. Zone VII was omitted from the survey to avoid disturbing nesting loons. Each zone was subdivided into three regions: Area A, characterized by a high density of pike (<1.0 m in depth); Area B, characterized by a low density of pike (1.0-3.0 m in depth); and Area C, characterized by the absence of pike (>3 m in depth). The strip census technique was applied using Areas A and B; Area C was eliminated from the survey.

All zones and areas were visually censused using a face mask and snorkel on five different 2-day sampling periods during the summer months (June, July, and August) of 1982. All surveys were conducted between 1000 and 1500 hours using the following census system. The first zone to be surveyed each sampling occasion was selected at random. The observer swam down the centre of Area A in the first zone counting all northern pike within an estimated 3-metre strip width, Area B in the adjacent zone, Area A in the third zone and so on until all zones were covered. The same procedure was carried out the following day on the complementary areas within each zone. Based on the clarity of the water, the crypticity and approachability of northern pike, and the screening effect of the habitat, a 3 metre strip width was considered to be optimal.

Accuracy of the estimation of strip width (distance) and depths were assessed by comparing 20 estimated depths and 20 estimated distances within the littoral zone to the actual depths and distances as measured directly by hand to within 1 centimetre. The mean difference between the estimated measurements and the actual measurements was determined. A paired t-test was used to test for significant differences between the estimated and true values (Sokal and Rohlf 1969 1973). Standard deviations (S.D.) are presented when estimates of the amount of variation are given for mean values.

Stratified systematic sampling was used because it is efficient in terms of the time and personnel required and tends to reduce the variability between samples thereby increasing the precision of the estimate (Struhsaker 1981). It was assumed that movement of pike between and within transects would be minimal during each sampling period; and as such, a systematic sampling regime allows one to sample without replacement during each 2-day interval and avoids the logistical difficulties of random sampling (Caughley 1977).

Population estimates were calculated for sampling period 1; sampling periods 1 and 2 (pooled); 1, 2, and 3 (pooled); 1, 2, 3, and 4 (pooled); and 1, 2, 3, 4, and 5 (pooled), following the formulae presented by Caughley (1977).

$\hat{y} = RZ$

$\hat{y}$ = estimated total population

N = total number of sampling units in the total area

n = number of transects surveyed

y_i = number of individuals on transect 'i'

z_i = area of transect 'i'

Z = total area under survey

$R = \Sigma y_i / \Sigma z_i$

When a systematic sample is drawn from a random population, the estimated population variance, $V(\hat{y})$ is approximately equal to the $V(\hat{y})$ based on simple random sampling. In addition, this method of calculating the estimated $V(\hat{y})$ can be used for variable plot size sampled with replacement (Seber 1973, Caughley 1977). When populations are clumped, this method may overestimate the true population variance (Mendenhall et al. 1971). The pike population of Roi Lake was concentrated in the littoral zone and was thus clumped with respect to depth distribution. The use of a stratified sampling scheme minimized the effect of this clumped pattern. Thus, the estimated variance of the population estimate and the 95 percent confidence limits for each estimate were calculated using formulae presented by Caughley (1977), and Seber (1973) for

estimates under a simple random sampling scheme.

$$V(\hat{y}) = (N^2 / n)s^2$$

where

$$s^2 = \Sigma(y_i - y)^2 / (n-1)$$

and

$$N = Z / (\Sigma z_i / n)$$

Estimates were computed for each stratum separately. Estimates for Areas A and B were then combined by summing the estimates for both strata and then summing the variances of the stratal estimates to give a variance of the combined estimate (Caughley 1977).

Depth Distribution

A major assumption in the stratified sampling design used is that the shallow littoral focus of pike abundance is constant throughout the period of investigation. To validate this assumption, an additional transect experiment was run concomitant with the population census to examine the depth distribution of northern pike.

Zone I was selected as the study site (Figure 1.1). Transect lines of yellow polypropylene rope (marked off at 1 metre intervals) were laid out parallel to the shoreline at 4 different depths from 0.6 to 4.8 metres in representative habitat areas. One transect (depth=0.6 m) was 200 metres in length; and the remaining three transects were 50 metres in length (Figure 1.1, Table 1.1). In terms of vegetation characteristics, habitat was homogeneous along the length of each transect. A strip width of 3 metres was used.

To examine month to month variation in the depth distribution of the adult pike (age 1 year or older) each transect was surveyed using snorkel and SCUBA 12 to 15 times during the daylight hours in the last 2 weeks of June, July, and August, approximately four times per month (daylight hours were defined as the hours of the day between the end of nautical sunrise and the beginning of nautical sunset, determined from the Nautical Almanac correcting for longitude and latitude (Anonymous 1980)). Transect 1 was also surveyed at various times in the first two weeks of July and August as part of the 'test for

independence' (outlined in a subsequent section). In addition, approximately 100 transects were surveyed across open water portions of the lake at various depths throughout the entirety of the sampling period. No pike were observed in these offshore waters.

Transect data were analyzed for homogeneity of counts for each transect within each 2 week sampling period using the chi-square test for homogeneity of replication (Bailey 1959):

x = number of fish in a given count
$\bar{x}$ = mean number of fish in a group of counts
k = number of counts in a group

$X^2 = \Sigma(x - \bar{x})^2/\bar{x}$ with $k-1$ degrees of freedom

In addition, depth distribution data were analyzed using a Kruskal-Wallis test for differences between transects in a given month and the Kruskal-Wallis multiple comparisions test for a posteriori comparisons between pairs of transects (Sokal and Rohlf 1969, Conover 1980). Data were considered to be significantly different at $P<0.05$.

Reaction of Pike to Observer Presence

A major concern in visual surveys is duplicate counts due to observer error and missed counts due to the hiding or dispersal of alerted fish in front of divers. To examine these sources of error as related to the underwater census of northern pike, the gross behavioral reaction of observed pike to the presence of the diver was recorded for each pike sighted on Transect 1, the transect characterized by the highest abundance of pike. Reaction was categorized as follows: no reaction, a slow retreat, or a dart. Chi-square analyses indicated that diver reaction was independent of day in June, July, and August. These homogeneous samples were thus pooled, and data were then analyzed using a chi-square test for independence of pike reaction with respect to month.

Test of Independence

A major assumption which underlies repeated surveys of transects is independence of samples ie. one must present evidence to indicate that the same fish are not being recorded on each census.

There was no evidence to indicate large-scale movements of pike throughout Roi Lake. However, qualitative observations in the preliminary survey suggested mixing of pike within a given area of the lake on a day to day basis. To assess the question of independence in a quantitative manner, a tagging study was carried out during the period of investigation. Forty northern pike (age 1 year or older) were tagged with sphaghetti dart tags (Floy Manufacturers, Seattle, Wash.) with a different tag color used in each zone. Fifty percent of these fish were captured and released in the Zone I study area. Each time Transect 1 was surveyed, the number of tagged fish, the color of the tag, and the estimated size of each fish was recorded (size estimates were accurate to within ±5 cm). A tagged fish sighted with a total length within ±5 centimetres of a tagged fish with the same tag color sighted on the previous survey, was considered to be a 'repeat' observation. The ratio of 'repeat' observations to the total number of tagged fish sighted was used as an estimate of repeatability.

C. RESULTS

Depth Distribution

Results of the chi-square tests for homogeneity of replication indicate that all counts were homogeneous ($P>0.05$, Table 1.2). This suggests that a series of three to six transect surveys made over a two week period was sufficient to produce reliable results with respect to the depth distribution of the adult pike.

The distribution of adult northern pike in relation to lake morphometry indicates selective use of shallow habitat in Roi Lake (Figure 1.2). There were significantly more adult pike on Transect 1 than on Transects 2, 3, and 4 during June, July, and August (Kruskal-Wallis tests, $P<0.05$). Consistent use of shallow water habitat throughout the summer months justifies the application of a stratified sampling regime for the estimation of population size.

Reaction of Northern Pike to Observer Presence

Reaction of pike to the presence of an observer was independent of month (X^2=4.39, df=4, 0.5>P>0.1, Figure 1.3). No apparent behavioral reaction to diver presence was exhibited by 64.7 percent of the observed pike, 31.7 percent retreated slowly into nearby cover, and 3.6 percent darted out of sight. Pike which exhibited a slow retreat were not considered to have been a source of error with respect to counts, as it was possible to monitor the position at which the fish finally settled. Pike which exhibited the 'dart reaction' may have been a possible source of error; however, a 4 percent error is not a significant problem compared to the variability of the final estimates.

Independence of Samples

A total of 47 tagged fish were sighted in the surveys of Transect 1 during the summer months. Six tagged fish were within ±5 centimetres of the total length of a marked fish (same tag color) sighted on the previous sampling occasion. This gives a maximum repeatability error estimate of:

6 / (47 - 4(fish sighted on last census, no subsequent sample)) x 100 = 14%

Therefore a maximum of 14 percent of the fish sighted on one census were likely observed in the subsequent survey. However, an average of 11 pike were sighted on Transect 1 during each survey, approximately 6 percent of the total estimated population (refer to final estimate). Thus, if mixing between samples was complete one would expect 6 percent repeatability. An additional 8 percent repeatability (as indicated in the test for independence) can be attributed to dependence between surveys i.e. samples were 92 percent independent, an adequate degree of independence to justify the use of the transect census technique with respect to this assumption.

Accuracy - Depth and Distance Estimates

The mean difference between the estimated distance measurements and the actual distance measurements (<3 m) was -0.45±11.5 centimetres (S.D., n=20), and there was no significant difference between the estimated and true values (paired t-test, t=-0.17, df=19, P=0.86). For depth measurements in less than 1 metre of water, the mean difference between the estimated and true values was 1.4±4.2 centimetres (S.D., n=10). For depths between 1 and 2 metres, the mean difference between the estimated and true values was -3.8±7.9 centimetres (S.D., n=10). There was no significant difference between the estimated and true distance measurements for depths less than 1 metre (paired t-test, t=-1.06, df=9, P=0.32) and depths between 1 and 2 metres (paired t-test, t=-1.52, df=9, P=0.16). As there was no significant difference between the estimated and true values, the estimation procedures used are considered appropriate for application to the strip census method.

Population Estimate

Population estimates for northern pike in Roi Lake are presented in Table 1.3. The final combined estimate for all five sample periods was 180±39 pike (95% C.I.). This represents a density of 23 northern pike per hectare of lake surface area and 96 pike per hectare of lake surface less than 3 metres in depth ('pike habitat'). The precision of a density estimate is usually expressed as the 95 percent confidence limits divided by the mean number of animals or groups per transect (Struhsaker 1981). However; as I have concentrated on population size rather than density, the precision of each estimate was calculated as the 95 percent confidence limits expressed as a percentage of the estimated population size. The precision curve presented in Figure 1.4 allows one to estimate the required sample size which maximizes precision and minimizes effort. The curve tends to level off at approximately n=24 suggesting that a sample in excess of 24 did not significantly improve the estimate.

D. DISCUSSION

Population Estimate

The population estimate based upon the pooled sample of all census intervals indicates a total of 180±39 adult pike (95% C.I.) in Roi Lake, a density of 23 pike per hectare of lake surface area and 96 pike per hectare of 'pike habitat'. This population density figure for the lake surface area is well within the range of estimates presented in published accounts (Table 1.4). A problem with comparing densities of fish per surface area of the water body relates to the pattern of habitat use or depth distribution exhibited by pike populations. Pike often inhabit the shallow littoral zone, and Grimm (1981) presented evidence to indicate that the standing stock of northern pike which a water body can support is directly related to the surface area of aquatic vegetation rather than the surface area of the water body. As such, densities per unit surface area of the water body may not reflect densities per surface area of available habitat. The density estimate for pike in less than 3 metres of water may more accurately represent the density of pike in Roi Lake.

The precision of the estimates increased with an increased sample size, showing a relationship typical of this sort of analysis (Struhsaker 1981). A sample size of 24 transects would be optimal in terms of precision of the estimate and survey efficiency for northern pike in Roi Lake.

Assumptions and Constraints: Depth Distribution, Reaction to Observer, Accuracy of Depth and Distribution Estimates, and Test of Independence

The chi-square tests for homogeneity of counts on a transects in a given month indicated that groups of 3 to 6 surveys over a 2 week period can produce a reliable estimate of the depth distribution of northern pike.

The consistency of the pattern of depth distribution over the 3 month period of the present investigation suggests that a population estimate can be based upon a stratified sampling regime in which data are collected in different sampling periods throughout the summer months.

The littoral distribution of pike in Roi Lake is in general agreement with a number of distribution related studies on the species. Diana et al. (1977) in an investigation of habitat use by northern pike in a relatively large, shallow, temperate lake, found that pike occupied water greater than 4 metres in depth less than 5 percent of the time and were associated with vegetation 95 percent of the time. Pike in a large mesotrophic lake of central Alberta, although relatively versatile in their habitat use, exhibited selection for shallow areas (Chapman and Mackay 1984a). Similarly, direct observation studies in two small, deep, pot-hole lakes in the same region indicated preferential use of shallow vegetated areas by northern pike (Chapman and Mackay 1984b, Turner unpubl. data).

Reaction of northern pike to the presence of an observer was low in all months with only 4 percent of the fish darting out of sight. To maintain a low level of disturbance it is necessary to census all transects at an extremely slow swimming speed (200m/20-30min). In addition, the observer must swim along the edge of emergent macrophytes, not through this type of vegetation. Qualitative observations indicated that any movement through the zone of emergent vegetation disturbed northern pike up to 5 metres in front of the observer.

There were no significant differences between the estimated distance and depth measurements and the actual distance and depth measurements. However if ropes were placed down at some predetermined depth and a fixed distance apart, estimation of depth and distance would not be necessary.

The estimate of repeatability based on a tagging investigation indicated that surveys of Transect 1 were 92 percent independent. The average interval between samples for the repeatability estimate was 3.5 days, and 11.8 days for the population estimates. Presumably, a larger inter-sample interval would result in a greater degree of mixing within the population and a lower proportion of 'repeat' observations. Thus, the repeatability estimate of 8 percent when extrapolated to the population census may be considered a conservative estimate.

E. CONCLUSIONS

(1) The visual census technique produced a final population estimate of 180±39 northern pike (95% C.I.) in Roi Lake, a density of 23 pike per hectare of lake surface area.

(2) A stratified systematic sampling design was suitable because of a constant depth distribution throughout the summer months, independence of samples, and minimal reaction of northern pike to diver presence.

(3) The efficiency and precision of the visual method and minimal physical disturbance of the fish population warrants use of this technique in estimates of relatively sedentary, littoral species in waters of sufficient clarity.

Table 1.1

Description of transects used to assess the depth distribution, pike in Roi Lake (Zone I study area).

TRANSECT NUMBER	MEAN DEPTH	DIMENSIONS	TRANSECT CHARACTERISTICS
T1	0.6 m	200 m x 3 m	67% _Scirpus_ 33% _Chara_
T2	1.7 m	50 m x 3 m	100% _Chara_
T3	2.9 m	50 m x 3 m	80% _Chara_ 20% ooze
T4	4.8 m	50 m x 3 m	100% ooze

Table 1.2

Chi-square tests for homogeneity of replication. Counts for a transect in a given month are considered homogeneous at $P > .05$.

TRANSECT NUMBER	MONTH	X^2	DEGREES OF FREEDOM	PROBABILITY VALUE
Transect 1	June	.07	2	P>0.9
	July	1.99	5	0.9>P>0.5
	Aug.	.50	3	P>0.9
Transect 2	June	0.00	2	P>0.9
	July	2.90	3	0.5>P>0.1
	Aug.	3.00	4	0.9>P>0.5
Transect 3	June	0.00	3	P>0.995
	July	6.12	6	0.5>P>0.1
	Aug.	0.00	2	P>0.995
Transect 4	June	0.00	4	P>0.995
	July	0.00	5	P>0.995
	Aug.	0.00	2	P>0.995

Table 1.3.

Population estimates for northern pike in Roi Lake, summer months, 1982.

Sample period 1: June 28-29
Sample period 2: July 8-9
Sample period 3: July 15-16
Sample period 4: July 26-27
Sample period 5: August 18-19

AREA A (<1 m)

SAMPLE	NUMBER OF TRANSECTS	$\hat{y}$	$V(\hat{y})$	95% CI
1	6	155.0	1679.6	105.4
1+2	12	144.2	506.4	49.5
1+2+3	18	157.8	512.0	47.7
1+2+3+4	24	184.0	454.3	44.1
1+2+3+4+5	30	173.3	367.3	39.2

AREA B (1-3 m)

SAMPLE	NUMBER OF TRANSECTS	$\hat{y}$	$V(\hat{y})$	95% CI
1	6	2.7	2.9	4.4
1+2	12	4.8	5.3	5.1
1+2+3	18	5.0	3.8	4.1
1+2+3+4	24	3.8	2.4	3.2
1+2+3+4+5	30	4.8	1.6	2.6

AREAS A+B

SAMPLE	NUMBER OF TRANSECTS	$\hat{y}$	$V(\hat{y})$	95% CI
1	12	157.7	1682.5	90.3
1+2	24	149.0	511.7	46.8
1+2+3	36	162.8	515.8	46.1
1+2+3+4	48	177.1	456.7	43.2
1+2+3+4+5	60	180.4	368.9	38.5

Table 1.4.

Population densities of northern pike in various north temperate waters. Where data were given as densities for different size or age classes, estimates are presented for pike age 1 year or older. Population estimates given over a number of years are expressed as a range.

NUMBER OF PIKE/HECTARE	SIZE OR AGE CLASSES INCLUDED	METHOD	LAKE OR RIVER	YEAR OF ESTIMATE	AUTHOR
10.1	>45 cm	Mark/ recap.	Slapton Ley, England	1975, 1976/77	Bregazzi and Kennedy (1980)
2.2-10.1	>22 in	Mark/ recap.	Escanaba Lake, Wisconsin	1959-1964	Kempinger and Carline (1978)
8.8	1+ or older	Mark/ recap.	Lake Windermere, England	1951	Kipling and Frost (1970)
8.3	2+ or older				
31.1-79.7	1+ or older	Mark/ recap.	River Frome, England	1971-1977	Mann (1980)
9.7	>15 cm	Rotenone	Loch Choin, Scotland	1955	Munro (1957)
29.4	>14 in	Mark/ recap.	Maple Lake Minnesota	1957-1958	Seaburg and Moyle (1964)
46.4	>10 in		Grove Lake Minnesota		
22.5	1+ or older	Strip census	Roi Lake, Alberta	1982	present study

Figure 1.1.

Roi Lake: macrophyte distribution, position of transect lines, and zone demarcation.

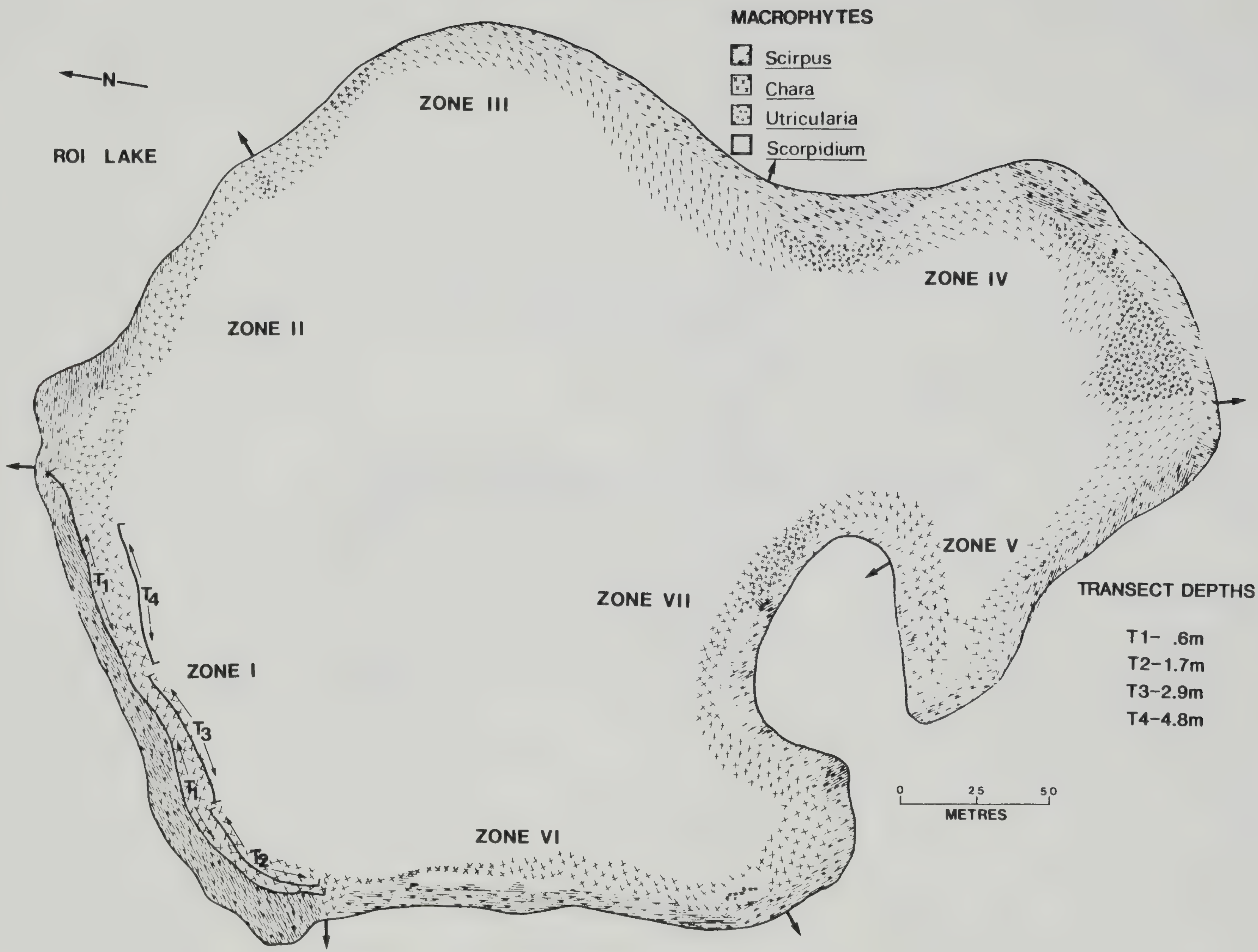
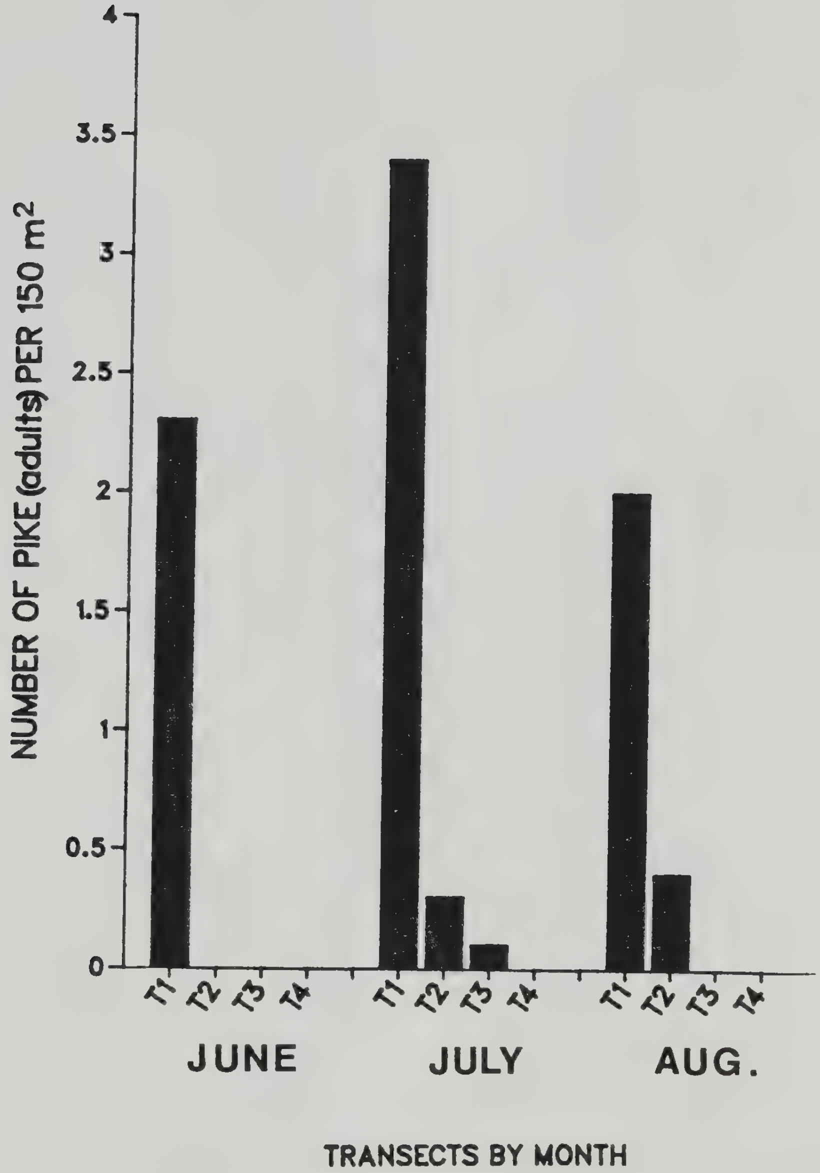

N
ROI LAKE
MACROPHYTES
Scirpus
Chara
Utricularia
Scorpidium
ZONE I
ZONE II
ZONE III
ZONE IV
ZONE V
ZONE VI
ZONE VII
T1
T4
T3
T1
T2
TRANSECT DEPTHS
T1- .6m
T2-1.7m
T3-2.9m
T4-4.8m
0
25
50
METRES

Figure 1.2.

Number of adult pike (age 1 year or older) observed on transects in Roi Lake during the summer months. Data were analyzed using a Kruskal-Wallis test for differences between transects in a given month and the Kruskal-Wallis multiple comparisons test for *a posteriori* comparisons between pairs of transects. Transect symbols underlined are not significantly different at $P<0.05$.

T1 - 0.6 m
T2 - 1.7 m
T3 - 2.9 m
T4 - 4.8 m



T1 T2 T3 T4 T1 T2 T3 T4 T1 T2 T3 T4

Figure 1.3.

Behavioral reaction of northern pike to the presence of an observer during June, July, and August in Roi Lake. The chi-square test was performed on the raw data (presented at the base of each bar); percentages have been used for graphic representation.

Ho: reaction of northern pike to diver presence is independent of month

$X^2=4.39$, $df=4$, $0.5>P>0.1$

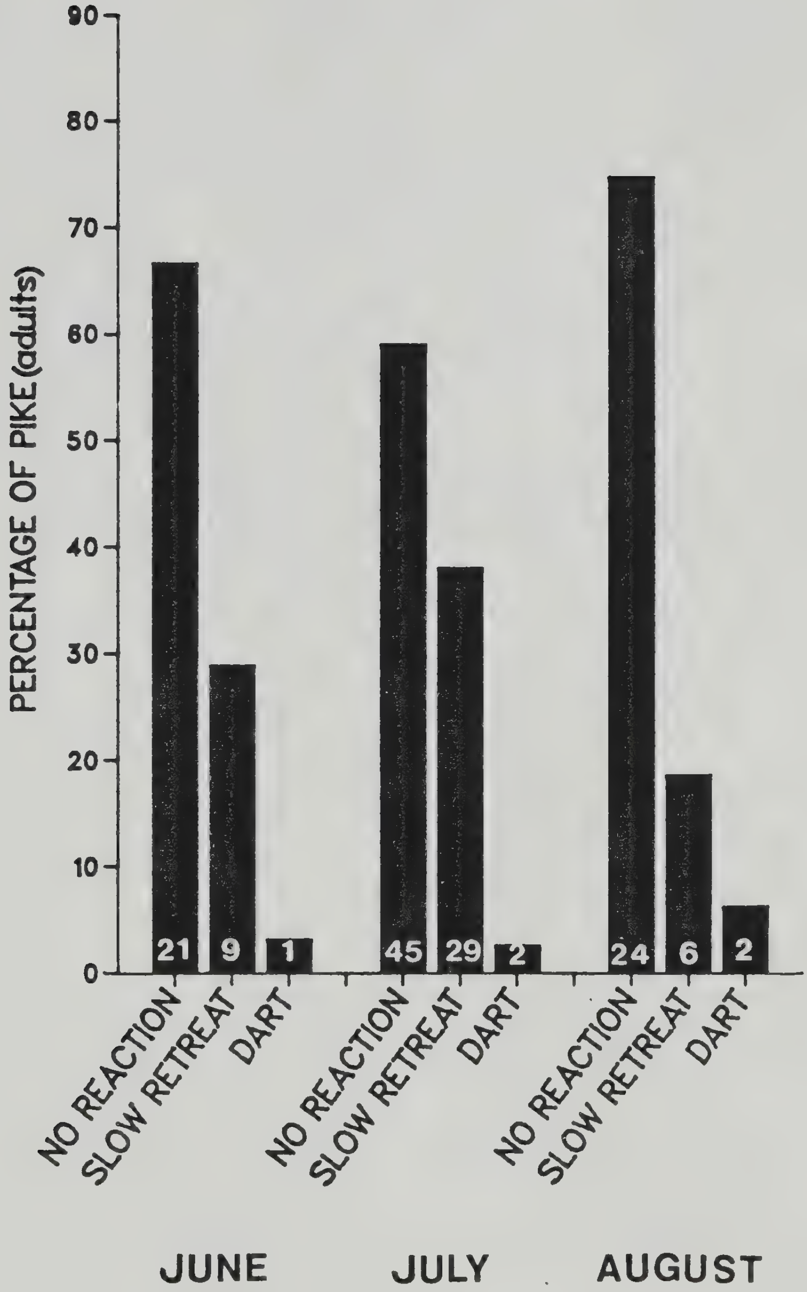
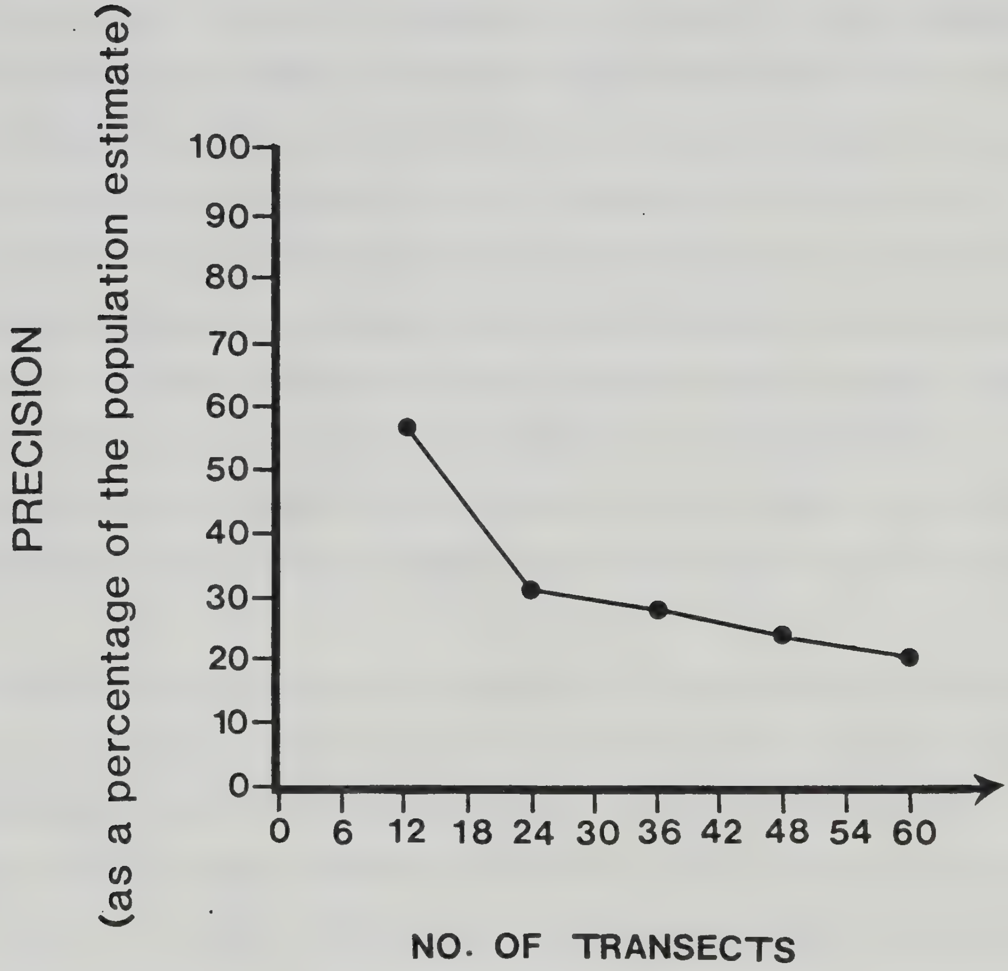

PERCENTAGE OF PIKE (adults)
90
80
70
60
50
40
30
20
10
0
21
9
1
45
29
2
24
6
2
NO REACTION
SLOW RETREAT
DART
NO REACTION
SLOW RETREAT
DART
NO REACTION
SLOW RETREAT
DART
JUNE
JULY
AUGUST

Figure 1.4.

Percentage precision of population estimates for northern pike (age 1 year or older) in Roi Lake, based on an increasing number of transects.

% Precision = (95% CI/$\bar{y}$) × 100


PRECISION
(as a percentage of the population estimate)
100
90
80
70
60
50
40
30
20
10
0
0
6
12
18
24
30
36
42
48
54
60
NO. OF TRANSECTS

II. SPATIAL AND TEMPORAL RESOURCE USE AND A SIZE-RELATED TROPHIC SHIFT IN THE NORTHERN PIKE OF ROI LAKE, ALBERTA

A. INTRODUCTION

The indeterminate nature of fish growth allows an individual to pass through more than one size-related phase of ecological relationships. In fact, on certain niche dimensions, intraspecific differences between size classes may be greater than interspecific differences. As such, development in fishes is often reflected in size-related spatial, temporal, dietary, and social changes which increase the complexity of inter- and intraspecific relationships and complicate the concept of niche as applied to a species description (Keast 1970, Werner et al. 1977, Helfman 1978, Keast 1978)

One of the best documented ontogenetic shifts in fish species is dietary change. This size-related phenomenon is considered to be the rule in fishes and has been described for a number of temperate freshwater species including perch, bluegill, crappie, largemouth bass, and walleye (Frost 1946, Frost 1954, Keast 1970, Keast 1977).

One would predict that many of the size-specific shifts in habitat use and activity patterns of temperate fishes would be highly correlated with these size-related trophic shifts.

The northern pike (Esox lucius) is a top predator in many freshwater ecosystems of the north-temperate region. Pike are very plastic with respect to foraging strategies exhibiting size-related trophic shifts (Hunt and Carbine 1950, Frost 1954, Munro 1957, Franklin and Smith 1963, Bregazzi and Kennedy 1980, Mann 1982), seasonal dietary shifts (Frost 1954, Lawler 1965, Mann 1982, Mackay unpubl. data), and major geographic differences in diet. Despite the highly variable nature of pike feeding habits, certain generalizations can be made with respect to size-related dietary changes. The pike is predominantly piscivorous at the end of the first summer; however, in some populations invertebrates may dominate the diet or appear on a seasonal basis (Healy 1956, Munro 1957, Christiansen 1976, Mackay unpubl. data). Among young-of-the-year pike, major changes in prey type may occur (eg. microcrustacea - larval aquatic insects - fish). By the time pike are 1 year old, they have, in general, assumed the adult mode of feeding.

Subsequent size-related changes in diet involve feeding on successively larger prey, larger species, or greater numbers of one prey type (Hunt and Carbine 1950, Frost 1954, Franklin and Smith 1963).

There have been numerous studies which have attempted to relate dietary shifts in northern pike, whether they be size-related, seasonal, or geographic differences in feeding habits, to the availability of prey species. Seasonal changes in the dietary characteristics of pike have been related to changing abundance levels of the major prey organisms (Frost 1954, Lawler 1965, Christiansen 1976, Mann 1982). Size-related trophic shifts have generally been attributed to the well-defined relationship between prey size and predator size i.e. organisms of the appropriate body size becoming available (Frost 1954, Diana 1979a, Mann 1982). However, there are few studies examining the relative importance of size-related shifts as determinants of activity and distribution patterns.

The objective of the present study was to assess the factors affecting the distribution and foraging activities of northern pike from a free-living population in which the dietary characteristics of juveniles (young-of-the-year) and adult pike (1 year or older) were markedly different. The major factors examined were a size-related trophic shift, water temperature, dissolved oxygen concentration, and aquatic macrophyte distribution. This approach allows one to examine the importance of prey use as a factor influencing the distribution and foraging rates of pike relative to additional variables which may affect these niche dimensions.

B. MATERIALS AND METHODS

Study Site

The research was conducted during June, July, and August of 1982 on Roi Lake, a small, unproductive, meromictic lake 40 km northwest of Edmonton, Alberta (53°51'N, 114°15'W). Roi lake has a surface area of 8 hectares, a maximum depth of 21 metres, and is characterized by a simple basin morphometry (Figure 2.1). The littoral zone was composed of a nearly continuous bench of the emergent macrophyte Scirpus extending as far as 20 metres from shore to a depth of 0.8 metres and a steep slope continuing to a depth of 5 metres dominated by the macroalga Chara. The lake was

thermally stratified with the metalimnion commencing at a depth of 4 to 5 metres, and characteristic of meromictic lakes, the hypolimnion is permanently anaerobic. A mean Secchi disk reading of 6.4±1.2 metres (standard deviation, n=20) was recorded during the period of investigation (Appendix I, Table 1).

Roi Lake supports populations of northern pike (Esox lucius), burbot (Lota lota, Iowa darters (Etheostoma exile), and a small number of brook stickleback (Culaea inconstans).

Descriptive Analyses - Distribution and Activity of Juvenile and Adult Pike

As a preliminary survey of the distribution of northern pike in Roi Lake, randomly selected areas of the lake were censused by snorkel and SCUBA (self-contained underwater breathing apparatus) in the first 2 weeks of June, 1982. Results of this survey indicated that 90 percent of the observed pike were associated with vegetation in less than 1.5 metres of water.

Based on the results of the preliminary census, a stratified sampling regime was used to assess temporal changes in the distribution and activity of northern pike on a monthly and hourly basis. A zone encompassing 1/7 of the littoral area was selected as the study site. Transect lines of yellow polypropylene rope (marked off at 1 metre intervals) were laid out parallel to the shoreline at four different depths from 0.6 to 4.8 metres in representative habitat areas. One transect (depth=0.6 m) was 200 metres in length, and the remaining transects were 50 metres in length (Figure 2.2, Table 2.1). In terms of vegetation characteristics, habitat was homogeneous along the length of each transect. Based on the clarity of the water, and approachability and crypticity of nothern pike, a 3 metre strip width was considered to be optimal.

To examine month to month variation in the distribution and activity of northern pike, each transect was surveyed using snorkel and SCUBA approximately 12 to 14 times during the daylight hours in the last 2 weeks of June, July, and August, approximately four times per month (daylight hours were defined as the hours of the day between the end of nautical sunrise and the beginning of nautical sunset, determined from the Nautical Almanac correcting for longitude and latitude (Anonymous 1980)). In addition, more than 100 transects were surveyed across open water portions of the lake at various depths

throughout the entirety of the sampling period. No pike were seen in the offshore waters. Pike were divided into two size classes, juveniles which included the young-of-the-year and adults which included pike age 1 year or older.

To examine habitat use and habitat selection on a finer scale than depth, the microhabitat used by the pike sighted on Transect 1 was recorded. This transect was in the area of highest pike abundance. Microhabitats were defined as areas at a given depth differentiated by vegetation characteristics. Transect 1, although homogeneous throughout its length could be divided into three microhabitat categories across its width: an area of emergent vegetation dominated by Scirpus, a strip of submergent vegetation dominated by Chara, and the interface area (approximately 40 centimetres wide) between the emergent and submergent vegetation. A fish was considered to be 'in' a specified microhabitat category if more than 1/2 of the body length of the fish was within the area.

Johnson (1966a) found northern pike to be active only in relation to actual feeding. Thus it was assumed that activity recorded as outlined would reflect rates of foraging activity. Whenever a pike was observed on a transect its activity status was recorded. A pike was considered active whenever it was moving either horizontally or vertically. Small postural movements were not considered as activity.

To examine temporal shifts in activity and microhabitat use on an hourly basis, transects were censused approximately four times in each of five different time periods during the daylight hours.

To describe the dispersion of adult and juvenile pike, the metre number at which each fish was sighted was recorded for pike observed on Transect 1. Five samples were taken in the last 2 weeks of July, and a total of 60 adults and 99 juveniles was recorded. A coefficient of dispersion (C.D.) was calculated for both juveniles and adults using 10 by 3 metre cells and 20 by 3 metre cells according to the formula presented by Sokal and Rohlf (1969). The value of the coefficient of dispersion will approximate 1 in Poisson distributions, will be greater than 1 in clumped samples, and less than 1 in cases of uniform dispersion (Southwood 1966, Sokal and Rohlf 1969).

$$\text{C.D.} = s^2 / \overline{y}$$

y_i= number of pike in sample cell 'i'

$\overline{y}$ = mean number of pike in each sample cell

$s^2 = \Sigma(y_i - \overline{y})^2 / n-1$

A significant departure of the coefficient of dispersion from unity implies a significant departure of the Poisson distribution from randomness, and this can be tested by calculating an index of dispersion (Id) where:

$$Id = s^2(n-1)/\overline{y}$$

The index of dispersion is distributed approximately as X^2 with n-1 degrees of freedom and can be used to test Ho: C.D.=1 (Southwood 1966, Sokal and Rohlf 1969). Rejection of the null hypothesis indicates a uniform or clumped dispersion pattern depending upon which tail of the chi-square distribution serves as the rejection region. If the null hypothesis is not rejected, a random distribution is a possibility (Southwood 1966, Sokal and Rohlf 1969, Gregory 1981). An index of dispersion was calculated for each sample date. The resultant indices were summed justified by the 'additive property' of X^2 (Bailey 1959). The degrees of freedom were calculated as the sum of the degrees of freedom for each sample date.

A systematic sampling regime was used to address the question; is the distribution of northern pike observed in Zone I representative of the entire lake? The littoral area of Roi Lake was divided into seven zones (Figure 2.2); Zone VII was omitted from the survey to avoid disturbing nesting loons. Each zone was divided into two morphometric areas for sampling: Area A which was less than 1.0 metres in depth and Area B which was 1.0 to 3.0 metres in depth. All zones and areas were visually censused on five different sampling occasions during the summer months.

Observations based on five night dives in the Zone I study area were used to qualitatively assess day-night shifts in the distribution and activity of the northern pike in Roi Lake.

The total length of each pike observed in the underwater census of Transects 1, 2, 3, and 4 was estimated. The accuracy of the estimate was determined by comparing the

estimated total length of each of 10 tagged pike to the recorded total lengths of these individuals measured to 0.1 centimetres.

Strengths and limitations of the underwater census technique in the estimation of the population size and the depth distribution of northern pike in Roi Lake have been previously described (Chapter I). A tagging study was used to validate the assumption of independence ie. that the same individuals were not observed on each sample day. Chi-square analysis indicated that habitat use and activity of northern pike were independent of the sample day for all months and for four of the five time periods examined. Results were pooled for these homogeneous samples.

Depth distribution data were analyzed using a Kruskal-Wallis test for differences within groups of more than two transects and the Kruskal-Wallis multiple comparisons test for a posteriori comparisons between pairs of transects. In the broadscale littoral survey, the Mann-Whitney U test was used to detect differences in pike numbers between Areas A and B (Sokal and Rohlf 1969, Conover 1980). Corrections were made for tied observations in both the Kruskal-Wallis and Mann-Whitney U tests. The chi-square contigency test was used to test for independence of microhabitat use and activity with respect to month and time period. The chi-square test for goodness of fit was used in the analysis of microhabitat selection. Standard deviations (S.D.) are presented when estimates of the amount of variation are given for mean values.

Environmental Factors

To examine the relationships between abiotic factors and the distribution and activity of pike in Roi Lake, water level, dissolved oxygen concentration, and water temperature were monitored throughout the summer months using standard limnological procedures.

Sampling regimes were designed to examine diurnal fluctuations for both dissolved oxygen concentration and water temperature and to describe water temperature profiles throughout the summer months. Diurnal fluctuations in these parameters were recorded at three stations within the study area: Station #1 in 0.5 metres of water in the zone of emergent vegetation, Station #2 in 4 metres of water over submergent vegetation, and Station #3 in the limnetic zone in 9 metres of water (Figure 2.1). Dissolved oxygen

concentration, measured using Winkler technique (Carpenter 1965), and water temperature, measured with a Montedoro-Whitney thermistor (accurate to 0.1 °C), were monitored every 4 hours between 0700 and 2300 hours four times during the course of the summer. Water samples were taken for oxygen determination and water temperature was recorded at 0 metres in the emergent vegetation zone; 0 and 3 metres in the submergent vegetation zone; and 0, 3, and 6 metres in the limnetic zone. Temperature profiles were collected on a weekly basis at four sampling sites (Figure 2.1).

Biotic Interactive Factors

To ensure an adequate sample of all size classes, northern pike were captured using three live-capture techniques: a trap net with a 10 metre lead net, a plastic bag net, and fly-fishing. Food habits were examined by flushing out the stomachs of pike using a modified version of the stomach pump described by Crossman and Hamilton (1978). Pike were anaesthetized using M.S.222 (tricaine methane sulfonate). The stomachs of juvenile pike were flushed with a micro-pipette once they reached a length of 8 centimetres. Attempts were made to sample pike in all five designated time periods. Adults were sampled between June 25 and August 23; juveniles were sampled between July 16 and September 15, 1982. There were no apparent changes in diet composition in either juveniles or adults over time.

Stomach contents were preserved in 10 percent formalin pending laboratory analysis. Contents were identified, and the length of each item was either measured or estimated when digestion precluded an accurate measurement.

Chi-square analysis was used to test whether diet was independent of trophic class with respect to the two major prey types consumed.

Effects of predator-prey interactions on the rate of foraging activity of juvenile and adult pike were examined indirectly through interpretation and further analyses of stomach content data. A Pearson correlation was used to test for a significant relationship between predator size and prey size, and predator size and the number of items consumed (Sokal and Rohlf 1969 1973).

The distribution and habitat use of the major prey species were examined through collection and census using snorkel and SCUBA. A sample of anisopterans, the major

prey items consumed by adult pike, was collected in less than 2 metres of water in randomly selected zones. All major habitat categories were represented in this depth stratum. Anisopterans were collected by snorkeling; and thus, the sample obtained reflects those nymphs which could be located visually. The total length of each dragonfly nymph was measured to the nearest millimetre for comparison with the total length of the nymphs consumed by the adult pike. The distribution of juvenile northern pike and the distribution of their major prey items, juvenile Iowa darters, was compared by ranking the relative abundance of the two species on transects within and immediately adjacent to the Zone I study area. A Spearman correlation was used to test for a significant correlation between the distribution of juvenile darters and juvenile pike (Zar 1974).

Selection for prey size by adult pike was examined through a statistical comparison of a size frequency histogram of the visually collected sample of dragonfly nymphs and a size frequency histogram of the consumed nymphs using a chi-square test for goodness of fit.

C. RESULTS

Distribution Patterns

A total of 332 juvenile pike and 203 adult pike were observed in the examination of depth distribution patterns, activity, and microhabitat use in the Zone I study area. The mean total lengths (estimated to within ±5 cm) of the juvenile pike and adult pike observed were 10.5±2.1 cm (S.D., n=320 range=4-17 cm) and 37.8±10.1 cm (S.D., n=193, range=18-60 cm), respectively.

The distribution of juvenile and adult northern pike in relation to lake morphometry suggests selective use of shallow habitat by pike in Roi Lake (Figure 2.3). There were significantly more adult and juvenile pike on Transect 1 than on Transects 2, 3, and 4 during June, July, and August (Kruskal-Wallis tests, $P<0.05$).

Use of shallow habitat by northern pike in Roi Lake is further supported by the broadscale survey of the littoral region. A total of 583 observations of northern pike was recorded in the littoral survey. In all zones censused, there was a significantly higher abundance of pike in Area A (<1.0 m) than in Area B (1.0 m - 3.0 m) (Mann-Whitney U

tests, $P<0.005$, Table 2.2).

There were no significant differences in microhabitat use between months or between time periods during the day for either juveniles or adults (Table 2.3). However, the data indicate differential habitat use between juveniles and adults ($X^2=7.81$, $df=2$, $0.025>P>0.01$, Figure 2.4). Juveniles showed slightly higher association with Chara than the adults, while the adults exhibited relatively high use of Scirpus beds.

An examination of microhabitat selection, rather than microhabitat use, demands a comparison of the observed habitat use and expected habitat use based on the proportion of available habitat in each microhabitat category. There was a significant difference between the observed and expected results for adults ($X^2=12.53$, $df=2$, $P<0.005$) and juveniles ($X^2=27.45$, $df=2$, $P<0.005$). Selection for the interface area between emergent and submergent vegetation was exhibited by both adults and juveniles. However, young-of-the-year, unlike adults, were observed in the area of submergent vegetation more than would be expected by chance and in the area of emergent vegetation less than would be expected by chance (Figure 2.5).

Chi-square analyses of dispersion data indicates that both adult and juvenile pike were not distributed randomly in space (Table 2.4). Juveniles exhibited a clumped pattern of distribution, while a uniform pattern was characteristic of the adult segment of the population. There was no discrepancy in results between the two cell sizes used in the analyses.

Qualitative observations based on five night dives indicated day-night alteration in the distribution and activity of northern pike in Roi Lake. This was characterized by some dispersal of pike into deeper waters, a depression in the level of activity, and a preference for the lower 1/3 of the water column. At night the majority of the fish sighted were in contact with the substrate. In addition, there was an apparent decrease in the sensitivity of the pike to external stimuli.

Activity Patterns

The percentage of inactive adult pike observed during the daylight hours of June, July, and August was high (89 to 91 percent), and there was no evidence to indicate changes in the proportion of inactive adults between months ($X^2=0.024$, $df=2$, $P>0.975$,

Figure 2.6). Similarly, the percentage of inactive juveniles was high (87 to 100 percent), and juveniles showed no change in activity level on a month to month basis (X^2=3.66, df=2, 0.5>P>0.1, Figure 2.6).

There was no evidence to indicate changes in the proportion of inactive adult pike between time periods during the daylight hours (X^2=3.87, df=3, 0.5>P>0.1, Figure 2.7). Similarly, the percentage of inactive juvenile pike was high and independent of time period (X^2= 3.53, df=3, 0.5>P>0.1, Figure 2.7). In addition, there was no significant difference between the proportion of inactive juveniles and the proportion of inactive adults based on a comparison of the pooled month by month observations for the two size classes (X^2=0.030, df=2, 0.9>P>0.5)..

Environmental Factors

Presence of Vegetation

Approximately 90 percent of the northern pike sighted were associated with vegetation and were in water less that 1 metre deep. As pike may be found in these vegetated areas because of some other depth-related factor such as temperature, it was necessary to further examine the influence of macrophytes on the distribution of pike. Transect 1 was compared to two transects placed in adjacent areas at comparable depths but with different vegetation characteristics. Transect 5 (50 metres in length) contained comparable proportions of emergent and submergent vegetation to Transect 1; however, the submergent vegetation was dominated by the moss Scorpidium. Transect 6 (25 metres in length) was characterized by a silt substrate and the absence of vegetation. Each transect was surveyed 12 to 14 times and a total of 170 observations of northern pike were recorded. There was no significant difference in the total number of pike observed on Transects 1 and 5 during June, July, and August (Kruskal Wallis tests, P<.05, Figure 2.8). However, only two pike were observed on Transect 6 throughout the entire sampling period. Thus, at a depth of less than 1 metre, vegetated areas were selected over areas where vegetation was absent.

Limnological factors

Changes in water level may increase or decrease the amount of available habitat for northern pike, particularly when the distribution of the population tends to be limited to the shallow littoral zone. In Roi Lake, the maximum recorded change in water level was 16.5 centimetres (Appendix I, Figure 1). However, there was no apparent change in the distribution or activity of the resident pike in response to this fluctuation.

Temperature profiles taken on a weekly basis indicated that Roi Lake was thermally stratified throughout the summer months with the metalimnion commencing at a depth of 4 to 5 metres throughout the lake (Appendix I, Table 2).

Diurnal fluctuations in temperature were most pronounced in the zone of emergent vegetation where temperatures were highest between 1400 and 1600 hours. The maximum diel change in temperature recorded over the course of the summer was 3.4 C^0 (Table 2.5).

A consideration of temperature data in light of the descriptive analyses of pike distribution in Roi Lake indicates that pike were associated with the warmest areas of the lake. During the daylight hours, northern pike were never sighted on Transect 4 which was located below the epilimnion, suggesting that temperature may have influenced the depth distribution of the pike. However, diurnal fluctuations in temperature did not appear to induce temporal shifts in the distribution or the activity of the pike during the daylight hours.

Roi Lake was anoxic below 8 to 9 metres and remained so throughout the summer months (Paul Murtaugh pers. comm.) An algal plate developed between 4.5 and 6 metres during the first week of July, and very high oxygen levels were associated with this depth stratum until fall turnover. Diurnal variations in dissolved oxygen concentration were most pronounced in the area of the algal plate (Table 2.5). The maximum diurnal change in oxygen concentration recorded over the course of the sampling program was 6.1 mg/L.

It would appear that dissolved oxygen concentration set ultimate bounds on the distribution of northern pike in Roi Lake, as the hypolimnion remained anoxic throughout the summer months. However, within the areas of the lake where oxygen was available, pike showed no apparent response to diurnal variation in dissolved oxygen concentration.

Biotic Interactions

Prey Use

The stomach contents of 44 adult pike (mean total length= 36.1±10.9 cm, S.D., n=44, range=18-67 cm) and 28 juvenile pike (mean total length=11.6±2.4 cm, S.D., n=27, range=8-18 cm) were examined. Prey use was determined by calculating the percentage of stomachs containing each category of food item, expressed as a percentage of all non-empty stomachs examined. The most frequent food items in the stomachs of adult pike were anisopterans (dragonfly nymphs) represented by two genera, _Aeshna_ and _Macromia_. _Aeshna_ comprised 90 percent of the nymphs consumed (Figure 2.9). Juvenile pike fed primarily on fish showing a marked preference for Iowa darters (_Etheostoma exile_) (Figure 2.9). All darters consumed by the juveniles were young-of-the-year.

The categories of food items were combined into two general classes of vertebrates and invertebrates. A chi-square test was used to test for a significant difference between the diet of the two trophic classes.

There was a significant difference in the diet of juveniles and adults with respect to the frequency of occurrence of the two food categories (X^2=12.17, df=1, P<.005, Figure 2.10) and percentage composition by number of individual items in each food category (X^2=65.26, df=1, P<0.005, Figure 2.10). Juveniles were feeding primarily on fish during the summer months, while adults exhibited an invertebrate-dominated diet.

Prey Distribution Relative to Pike

To examine the habitat use of prey items visually available to the adult pike, a random sample of anisopterans was collected by snorkelling in less than 2 metres of water. All major habitat categories were represented in this depth stratum. The majority of the nymphs were found in association with submergent vegetation, a habitat neither heavily used nor selected by the adult pike (Figure 2.11).

The distribution of juvenile Iowa darters and juvenile northern pike was compared by ranking the relative abundance of the two species on Transects 1 through 6. There was no correlation between the distribution of the juvenile pike and the distribution of their major prey items (Spearman Corr., P=0.479, Figure 2.12).

Prey type and pike foraging rates

The effects of predator-prey interactions on the rates of foraging activity by northern pike were derived indirectly through further analyses of stomach content data. Rate of foraging activity was considered to be the intake of food items per unit of time.

Adult pike showed a low percentage of empty stomachs (29.5%) and of those adult pike which had food in their stomachs, 74 percent contained two or more items. The juvenile fish-eating segment of the population exhibited a high percentage of empty stomachs (54.0%), and all stomachs contained two or less food items. A high percentage of empty stomachs and a low number of food items in juveniles relative to adults provides indirect evidence to indicate that the foraging rate of the adult invertebrate-feeding segment of the population was higher than the foraging rate of the piscivorous juveniles.

With respect to the adult sample, there was no correlation between the total length of predator and total length of prey ($r^2=0.0001$, $P=0.48$), but there was a positive correlation between number of items consumed and the predator size ($r^2=0.28$, $P<0.01$). A statistical comparison of a size frequency histogram of dragonfly nymphs consumed by adult pike to a size frequency histogram of the random sample of dragonfly nymphs collected visually indicates that adult pike consumed larger nymphs than would be expected by chance ($X^2=122.58$, df=4, $P<0.005$, Figure 2.13). Assuming that the size frequency histogram of the random sample reflects the frequencies available to the pike, this suggests selection for large prey size. However, all size categories of adult pike are able to consume items much larger than dragonfly nymphs (as observed in piscivorous populations); and thus, selection for large prey size did not result in the positive predator-prey size relationship characteristic of piscivorous populations. As all adult pike tended to feed on small organisms, large pike necessarily consumed greater numbers of prey items than small adults providing support for a size-related increase in foraging activity within the adult segment of the population.

D. DISCUSSION

Distribution Patterns, Microhabitat Use, and Microhabitat Selection

An integration of the factors considered as possible determinants of pike distribution patterns in Roi Lake would suggest that water temperature, dissolved oxygen concentration, and the presence of vegetation may have set overall bounds on the depth distribution of the study population. Within the selected depth stratum, vegetation characteristics and ecological interactions were probably responsible for the finer resolution of microhabitat use among the size classes of northern pike.

The littoral distribution of northern pike in Roi Lake is in general agreement with a number of distribution-related studies on the species. Diana et al. (1977) in an investigation of habitat use by northern pike in a relatively large, shallow temperate lake (Lac Ste. Anne, Alberta), found that pike occupied water more than 4 metres deep less than 5 percent of the time and were associated with aquatic vegetation 95 percent of the time. Similarly, pike in Seibert Lake, a large, mesotrophic lake of central Alberta, although relatively versatile in their habitat use, exhibited selection for vegetated shallow areas (Chapman and Mackay 1984a). Johnson (1966b) suggested that the pike of Lake Windermere, England inhabited much of the inshore area and were restricted to depths of less than 6.5 metres.

The selection exhibited by the northern pike in Roi Lake for vegetated areas over areas where macrophytes were absent emphasizes the importance of vegetation as a primary determinant of distribution pattern in this population. Grimm (1981b, 1983) in a study of four stocked ponds, concluded that vegetated areas are preferred habitat for northern pike; and he presented evidence to suggest that the abundance of vegetation is a limiting factor controlling the biomass of small pike.

In Roi Lake, northern pike were always observed in the epilimnion during the daylight hours; and thus the thermocline may have served as a daytime (but not nighttime) barrier to movement of the pike. This is in agreement with the observations of Helfman (1979) on a number of fish species in Cazenovia Lake, New York.

Oxygen set ultimate bounds on the distribution of pike in Roi Lake, as the hypolimnion was permanently anoxic. It has been reported that fish may swim into anoxic

waters to forage (Hasler 1945); however, there was no evidence of such feeding excursions in Roi Lake.

Although the distribution of juvenile and adult pike was similar with respect to depth characteristics and the general association with vegetation; there was evidence of differences between adults and juveniles in microhabitat use, microhabitat selection, and dispersion pattern.

It is conceivable that the predominantly marginal distribution of the adult pike in Roi Lake may be partially explained by littoral distribution of its invertebrate prey. Keast and Harker (1977a) in an examination of benthic invertebrate biomass relative to depth in Lake Opinicon, Ontario, reported that 68 percent of the invertebrate biomass was concentrated in the littoral zone between 0 and 2.5 metres. They found a close link between the distribution of specific prey organisms and various fish species. Makowecki (1973) found that the invertebrates which dominated the diet of small pike in Seibert Lake, Alberta were most abundant in the shallow vegetated regions, the preferred habitat of the young pike.

However, a consideration of habitat use on a finer scale than depth suggests little overlap between predator and prey. The microhabitat most heavily used by adult pike in Roi Lake was the zone of emergent vegetation, and adults showed selection for the edge area between the emergent and submergent vegetation. Dragonfly nymphs were observed primarily in the area of submergent vegetation, a habitat neither heavily used nor selected by the adult pike. This area, which has an extremely dense growth of Chara, is not easily penetrated by larger pike (pers. obs.). Northern pike generally use a specialized stalking-lunge attack which has been described by Hoogland et al. (1956) and Nursall (1973). Webb and Skadsen (1980) presented evidence to indicate that these foraging tactics of Esox are genetically determined. Taking into account the predatory lurking-ambush strategy of northern pike, the 'Chara' habitat may not provide adequate cover for the adults. The zone of emergent vegetation and the selected edge area between the emergent Scirpus and submergent Chara vegetation would afford a high degree of cover, a characteristic compatible with the predatory strategies of northern pike.

Both juvenile pike and their major prey items, juvenile darters were restricted in their distribution to the littoral zone; however, within this area there was no evidence of a relationship between the habitat of predator and prey. Transects characterized by a high relative abundance of darters were characterized by a low relative abundance of juvenile pike and visa versa. Iowa darters were observed in highest abundance on Transect 6. This transect was characterized by the absence of vegetation, a factor of apparent importance in habitat selection by pike.

Intraspecific predation may be an important force in the selection of microhabitat by juvenile pike in Roi Lake. With respect to microhabitat, young-of-the-year pike showed selection for the interface area between emergent and submergent vegetation and the Chara habitat and were found in the area of emergent vegetation less than would be expected by chance. Selection of these two microhabitats may reflect an anti-predator strategy. When juvenile pike were disturbed by observer presence or purposefully chased, the most frequent response was a dart into the submergent Chara, a dense cover which could be penetrated by the juveniles and which in most cases completely obliterated any visual sign of the fish. Potential predators of young-of-the-year pike in Roi Lake include muskrat, resident loons, and conspecifics (there was a 6.5 percent frequency of occurrence of young-of-the-year pike in the stomachs of adult pike).

It has been suggested in related studies that size-specific differences in the spatial distribution of fish species may be associated with mechanisms for the avoidance of predation. Cannibalism, an extreme form of size-related predation pressure, may lead to selection for the avoidance of conspecific predators and a strong defense repertoire (Fox 1975, Hall and Werner 1977, Werner et al. 1977, Helfman 1978). Selection for dense cover, speculated as an antipredator strategy, has been observed in many small temperate fish species and the young of numerous larger species (Hall and Werner 1977, Werner et al. 1977, Helfman 1978, Keast 1978, Fraser and Cerri 1982).

Intraspecific predation has been documented for a number of northern pike populations (Frost 1954, Lagler 1956, Munro 1957, Lawler 1965) and may serve a function in biomass regulation (Grimm 1983). Grimm (1981a, 1981b), found that small pike were restricted to vegetated areas; while large pike used both the open water and vegetated habitat. Grimm suggested that the function of shelter from intraspecific

predation may be significant as a determinant of habitat use by northern pike.

Christiansen (1976) observed the behavior of a number of prey species of northern pike in Kakisa Lake, N.W.T. and concluded that juvenile pike possessed the widest array of anti-predatory behaviors in response to predation pressure by adult pike. Juveniles of Kakisa Lake exhibited avoidance behaviors in the presence of adult pike and were observed primarily in very shallow water along vegetated shoreline areas.

In addition to the selection of dense cover, the clumped dispersion pattern of the juvenile pike may contribute to the avoidance of intraspecific predation. As Transect 1, used in the evaluation of dispersion pattern, was homogeneous throughout its length, it is probable that observed clumps of juveniles were not associated with a patchy distribution of resources but were of a social facilitation. It is generally considered that aggregations may serve as an anti-predator strategy by increasing the awareness of the potential prey to predatory stimuli (Radakov 1973, Krebs 1978, Keenleyside 1979). In further support, Neill and Cullen (1974) showed that predatory success of northern pike was highest when hunting a single fish.

The dispersion pattern of the juveniles was in contrast to that exhibited by the adult pike in the Roi Lake population. However, the uniform pattern observed in the adults is compatible with the solitary nature of northern pike (Christiansen 1976) and suggests an individual distance or space requirement (Southwood 1966, Ricklefs 1976). Christiansen (1976) in an examination of the social behavior of northern pike concluded that these fish spend a major portion of the daylight hours visually isolated from one another. Overdispersion in the adult segment of the Roi Lake population may facilitate both visual and physical isolation.

Activity Pattern and Foraging Rate

It is well documented in the literature that northern pike are primarily visual predators (Hoogland et al. 1956, Nursall 1973, Christiansen 1976) and are relatively inactive at night (Malinin 1969 1970, Diana 1980, Mackay unpubl. data) Although crepuscular periods are often favored for foraging activities by top predators (Hobson 1972 1974) temperate predators do not exhibit visual specialization for predatory activities during the twilight periods of rapidly changing levels of light intensity (Helfman

1979). And, in addition, the typically low water clarity of temperate lakes would reduce any visual advantage of a twilight predator (Helfman 1979). Thus, it was assumed in the present study that any rhythmicity in the activity of northern pike as related to prey use would occur during the daylight hours justified by the diurnal nature of this species and the related visual mode of feeding.

Pike in Roi Lake were inactive approximately 90 percent of the time during the daylight hours. This level remained constant throughout the summer months, and there were no differences between juveniles and adults. Christiansen (1976) reported a basic behavior pattern for northern pike characterized by extended periods of inactivity punctuated by periods of activity; active intervals comprising from 20 to 40 percent of the daylight hours. In addition, Christiansen observed a daily bimodal pattern of activity in northern pike during the daylight hours with peak levels in the midday and early evening. Similarly, Diana (1980) observed pike to be inactive over 80 percent of the time during the day. However, no regular diel changes in pike activity were recorded with the exception of inactivity at night. Malinin (1969) reported a marked diurnal activity pattern in northern pike with activity peaks in the morning and evening and complete inactivity at night. The results of this study would tend to agree most closely with those of Diana (1980). The higher levels of inactivity observed in the Roi Lake population may be related to the point-in-time sampling scheme which tends to underestimate 'time-active' when activity bouts are short (Jacobson and Wiggins 1982). Discrepancies in the description of pike activity patterns between related studies may be attributed to differential methodology, geographical variation, and differences in the type or scale of activity measured.

The juveniles in Roi Lake showed a high percentage of empty stomachs and a small number of food items per stomach. The small size range within the juvenile segment of the population precluded the possibility of looking for a relationship between predator size and prey size within this trophic class. The adult invertebrate-feeding segment of the population exhibited a low percentage of empty stomachs, no correlation between prey size and predator size, and a positive correlation between numbers of items consumed and predator size. These stomach content characteristics are obviously related to the observed adult diet of small organisms which require more time to collect in the larger numbers necessary, and thus less time for the stomach to be empty than in the juvenile

fish.

Additionally, Diana (1979b) reported a significantly higher caloric ration in female than male pike and concluded that the higher female rations were due to larger meals and not due to increased feeding frequencies. If higher female rations are characteristic of pike populations; it is conceivable that the foraging activities of female pike in Roi Lake, where there is no relationship between prey size and predator size, may be necessarily higher than the foraging rates of males. Such a phenomenon may account for a weak relationship between predator size and number of prey items consumed.

Review of literature on various pike populations reveals three important characteristics with respect to the stomach contents of piscivorous populations. First, there tends to be a high proportion of empty stomachs (Frost 1954, Seaburg and Moyle 1964, Shafi and Maitland 1971, Nursall 1973, Mann 1976, Diana 1979b). Secondly, stomachs generally contain a small number of food items (Diana 1979b, Mann 1982); and finally, there tends to be a positive correlation between prey size and predator size (Frost 1954, Popova 1966, Mann 1976, Diana 1979b). The juveniles of Roi Lake exhibited stomach content characteristics typical of pike populations with fish dominated diets; while the adult invertebrate-feeding component of the population did not conform to the three generalizations with respect to piscivorous pike populations. If activity levels as quantified in the subject study reflected rates of foraging activity, higher levels of activity should have been seen in the invertebrate-feeding adult pike than in the piscivorous juveniles. However, there was no significant difference in the proportion of inactive adults and the proportion of inactive juveniles, suggesting that activity did not adequately reflect rates of foraging activity.

Day-night Shifts

The northern pike in Roi lake did not show the strong attraction to structure at night typical of daytime patterns. Although a number of pike did rest in weedbeds during the hours of darkness, many more were exposed occupying areas below the epilimnion characterized by the absence of vegetation. This relaxation of structure-association emphasizes the importance of cover during the daylight hours either as an anti-predator or foraging strategy.

Muller (1978) concluded that the most important factor influencing the diel activity of fish is the alteration between light and darkness. Although other factors may determine the amount or rate of activity, light seems to play a signal role with respect to phase position (Manteifel et al. 1978, Muller 1978).

Emery (1973) reported pronounced day-night shifts in the distribution of a number of temperate fish species associated with a decrease in sensitivity to external stimuli, color changes, and contact with the substrate. The observed day-night shift in the activity and distribution of northern pike in Roi Lake is in agreement with the trends presented by Emery (1973) and Muller (1978) and is further supported by the research of Helfman (1979) who reported changes in the distribution and activity patterns of a number of diurnal temperate lake species associated with the alteration between light and darkness.

Night dispersal of diurnal fish into deeper areas characterized by cooler temperatures may be bioenergetically advantageous. Studies on the growth of sockeye salmon (Oncorhynchus nerka) indicated that food conversion efficiency remains high, and maintenance metabolism is much reduced at lower temperatures (Brett 1971, Biette and Geen 1980). Bioenergetic considerations may partially explain the observed night dispersal of some northern pike to areas below the epilimnion.

Size-related Trophic Shifts as Related to the Temporal Partitioning of Spatial Resources and Foraging Rates: an Integration

The results of this investigation into the temporal partitioning of spatial resources among two distinct trophic classes of northern pike in Roi Lake provides considerable insight into the nature of size-related resource shifts in this species. It was hypothesized that a size-associated trophic shift would be reflected in differential distribution and activity patterns between the trophic classes. It would appear that the presence of vegetation, water temperature, and dissolved oxygen concentration influenced the depth distribution of both juvenile and adult pike in Roi Lake. However, ecological interactions appear to have been responsible for the finer resolution of microhabitat use, intraspecific predation pressure in the case of the juveniles, and foraging strategies in the case of the adult pike. The size-related trophic shift from a piscivorous diet to an invertebrate dominated diet was reflected in an increased rate of foraging activity in the adult segment

of the population attributed to a diet of small organisms which were necessarily consumed in greater numbers than the prey items of the juvenile pike.

Table 2.1

Description of transects used to assess the depth distribution, microhabitat use, and activity of northern pike in Roi Lake (Zone I study area).

TRANSECT NUMBER	MEAN DEPTH	DIMENSIONS	TRANSECT CHARACTERISTICS
T1	0.6 m	200 m × 3 m	67% *Scirpus* 33% *Chara*
T2	1.7 m	50 m × 3 m	100% *Chara*
T3	2.9 m	50 m × 3 m	80% *Chara* 20% ooze
T4	4.8 m	50 m × 3 m	100% ooze

Table 2.2.

Number of pike observed per 600 m^2 in Area A (<1.0 m) and Area B (1.0-3.0 m) of six surveyed zones (150-200 m in length) in the littoral zone of Roi Lake. Averages are derived from a series of five surveys taken between June 18 and Aug. 19, 1982. Data were analyzed using the Mann-Whitney U test for differences between Areas A and B.

ZONE	AREA	AVERAGE NUMBER OF PIKE/600 m^2	MANN-WHITNEY U STATISTIC	PROB. LEVEL
I	A	23.0	25	P<0.005
	B	3.0		
II	A	12.9	25	P<0.005
	B	.5		
III	A	12.2	25	P<0.005
	B	1.2		
IV	A	17.6	25	P<0.005
	B	3.8		
V	A	22.6	25	P<0.005
	B	3.4		
VI	A	24.3	25	P<0.005
	B	2.7		

Table 2.3.

Chi-square analyses for differences in microhabitat use between months or time periods during the day for juveniles and adults.

Ho	TROPHIC CLASS	X^2 VALUE	DEGREES OF FREEDOM	PROBABILITY LEVEL
Microhabitat use is independent of month	Juveniles	7.36	4	$0.5>P>0.1$
	Adults	1.45	4	$0.9>P>0.5$
Microhabitat use is independent of time inverval	Juveniles	10.47	8	$0.5>P>0.1$
	Adults	2.70	8	$P>0.9$

Table 2.4.

Dispersion pattern analysis for adult and juvenile pike on Transect 1 in Roi Lake, July, 1982.

JUVENILES

CELL SIZE	DATE	C.D.*	Id*	X^2 VALUE	DEGREES OF FREEDOM	PROB. VALUE	DISPERSION PATTERN
10 m x 3 m (n=20)	July 14	1.38	26.26				
	July 15	1.51	28.67				
	July 20	1.36	25.76	131.3	95	0.01>P>0.005	Clumped
	July 22	1.18	22.23				
	July 26	1.49	28.23				
20 m x 3 m (n=10)	July 14	1.57	14.16				
	July 15	2.20	19.78				
	July 20	1.26	11.35	99.8	45	P<0.005	Clumped
	July 22	1.21	10.85				
	July 26	2.26	20.31				

ADULTS

CELL SIZE	DATE	C.D.*	Id*	X^2 VALUE	DEGREES OF FREEDOM	PROB. VALUE	DISPERSION PATTERN
10 m x 3 m (n=20)	July 14	.58	11.00				
	July 15	.64	12.22				
	July 20	.52	9.80	67.9	95	0.025>P>0.005	Uniform
	July 22	1.07	20.29				
	July 26	.77	14.57				
20 m x 3 m (n=10)	July 14	.85	7.67				
	July 15	.93	8.33				
	July 20	.31	2.75	35.7	45	0.10>P>0.025	Uniform
	July 22	.69	6.23				
	July 26	.67	6.00				

C.D.* - Coefficient of dispersion

Id* - Index of dispersion

Table 2.5.

Diurnal fluctuations in water temperature and dissolved oxygen concentration in Roi Lake during the summer months (values are the average of duplicate samples).

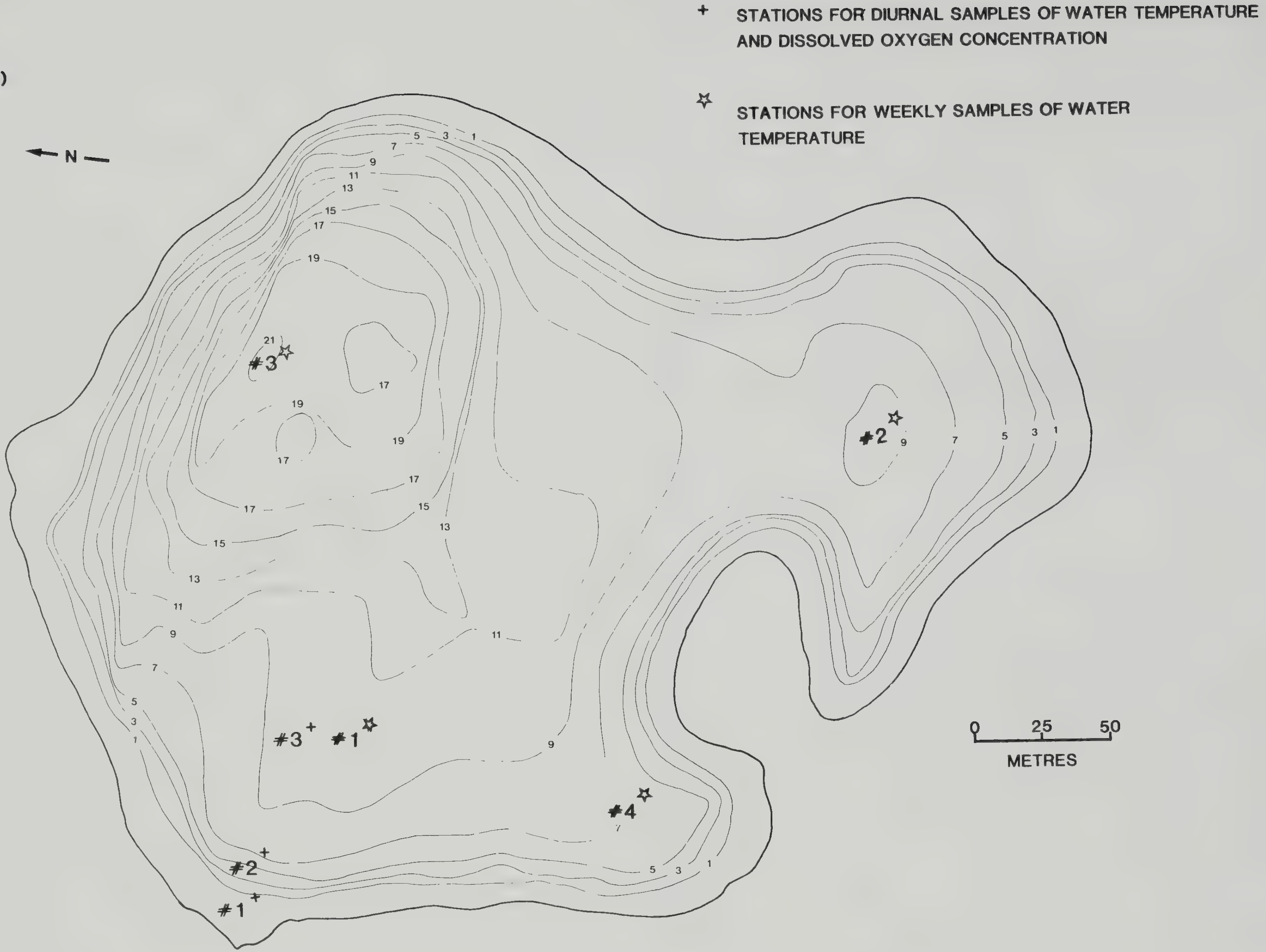
DATE	STATION NUMBER	DEPTH(m)	TIME				
			0700	1100	1500	1900	2300
			T(°C) $[O_2]$(mg/L)	T(°C) $[O_2]$(mg/L)	T(°C) $[O_2]$(mg/L)	T(°C) $[O_2]$(mg/L)	T(°C) $[O_2]$(mg/L)
June 8	#1	0	14.3	15.4	16.0	16.5	15.4
		0	10.8	11.4	12.4	13.7	11.4
	#2	0	14.6	15.1	15.5	15.8	15.3
		0	10.9	11.0	11.6	12.1	11.5
		3	14.5	14.7	15.0	14.9	15.0
		3	10.6	10.8	10.5	11.8	11.2
	#3	0	14.7	15.1	15.7	15.5	15.3
		0	10.9	11.0	10.8	11.0	11.1
		3	14.5	14.6	14.9	14.7	14.8
		3	10.8	11.0	10.4	11.6	10.9
		6	****	7.7	7.8	7.8	7.5
		6	7.5	8.2	8.3	8.9	8.3
June 26	#1	0	18.9	20.0	22.3	21.7	20.7
		0	10.2	****	10.1	10.7	10.4
	#2	0	19.4	19.8	21.8	21.7	20.8
		0	10.1	****	10.5	10.4	10.6
		3	19.4	19.8	19.8	19.6	19.4
		3	9.7	****	11.1	12.0	11.2
	#3	0	19.3	19.7	21.5	21.7	20.8
		0	10.6	****	10.4	10.4	10.5
		3	19.1	19.4	19.6	19.7	19.5
		3	14.2	****	14.5	13.1	11.9
		6	8.7	9.2	9.4	9.2	9.2
		6	10.8	****	10.6	10.5	10.9
July 21	#1	0	19.2	19.3	21.0	20.4	19.6
		0	8.9	8.9	9.4	8.6	8.6
	#2	0	19.4	19.4	20.5	****	19.7
		0	8.8	9.0	9.5	9.2	8.9
		3	19.3	19.4	19.9	****	19.5
		3	8.9	8.8	9.0	9.1	10.0
	#3	0	19.3	19.4	19.7	21.0	19.6
		0	9.6	9.1	9.1	9.1	9.5
		3	19.2	19.3	19.7	19.7	19.6
		3	8.9	9.0	9.1	9.0	9.3
		6	10.3	11.4	10.5	10.8	10.7
		6	13.9	12.6	14.4	15.9	16.6
Aug.2	#1	0	21.1	21.4	22.0	21.5	20.9
		0	8.2	8.5	8.7	8.9	8.9
	#2	0	21.1	21.3	21.8	21.4	21.2
		0	8.3	8.5	8.7	8.9	8.9
		3	20.1	20.9	21.3	20.8	21.5
		3	7.5	8.8	8.7	8.9	9.1
	#3	0	21.2	21.3	21.4	21.4	21.4
		0	8.6	8.5	9.5	8.4	8.6
		3	20.9	20.7	20.7	20.9	20.4
		3	9.0	9.2	9.3	9.1	****
		6	11.5	12.1	11.8	11.5	****
		6	8.7	12.8	13.1	14.0	14.8

Figure 2.1.

Bathymetric map of Roi Lake, data obtained by hand sounding 20 transects at 5 metre intervals.

ROI LAKE

(DEPTH IN METRES)



N
+ STATIONS FOR DIURNAL SAMPLES OF WATER TEMPERATURE AND DISSOLVED OXYGEN CONCENTRATION
☆ STATIONS FOR WEEKLY SAMPLES OF WATER TEMPERATURE
0
25
50
METRES
#1
#2
#3
#4
1
3
5
7
9
11
13
15
17
19
21

Figure 2.2.

Roi Lake: macrophyte distribution, position of transect lines, and zone demarcation.

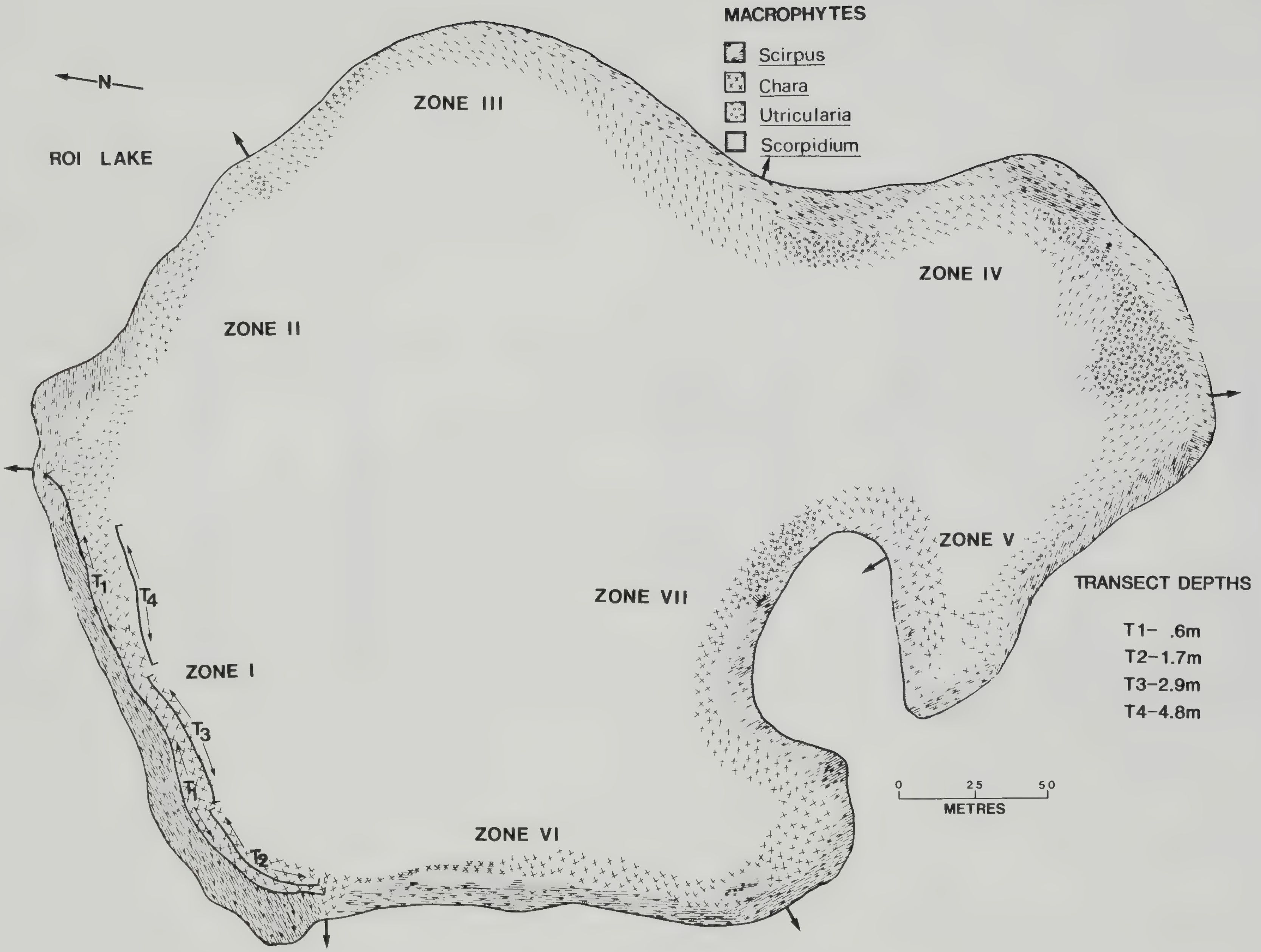
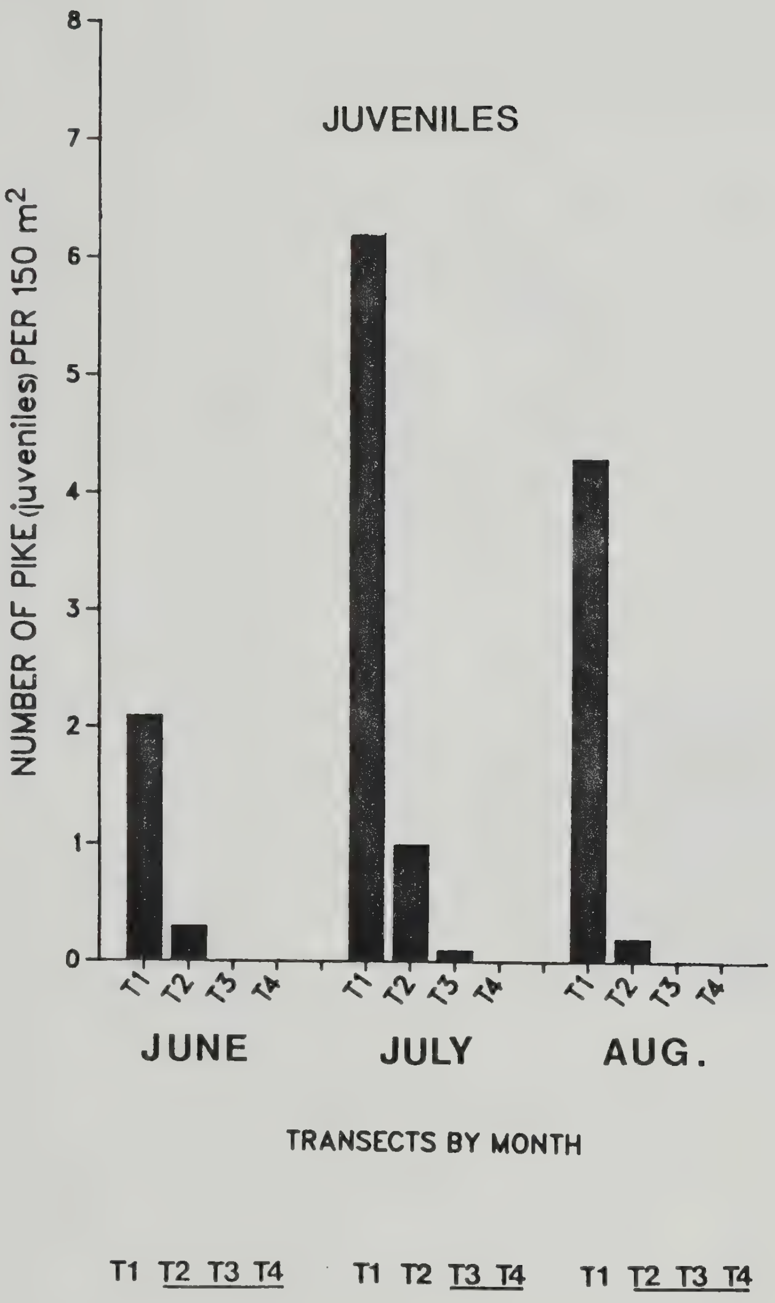

N
ROI LAKE
MACROPHYTES
Scirpus
Chara
Utricularia
Scorpidium
ZONE I
ZONE II
ZONE III
ZONE IV
ZONE V
ZONE VI
ZONE VII
T1
T4
T3
T1
T2
TRANSECT DEPTHS
T1- .6m
T2-1.7m
T3-2.9m
T4-4.8m
0
25
50
METRES

Figure 2.3

Number of adult and juvenile pike observed on transects during the summer months. Data were analyzed using a Kruskal-Wallis test for differences between transects in a given month and the Kruskal-Wallis multiple comparisons test for a posteriori comparisons between pairs of transects. Transect symbols underlined are not significantly different at P<0.05.

T1 - 0.6 m
T2 - 1.7 m
T3 - 2.9 m
T4 - 4.8 m


JUVENILES
NUMBER OF PIKE (juveniles) PER 150 m2
0
1
2
3
4
5
6
7
8
T1
T2
T3
T4
JUNE
JULY
AUG.
TRANSECTS BY MONTH
T1 T2 T3 T4
T1 T2 T3 T4
T1 T2 T3 T4

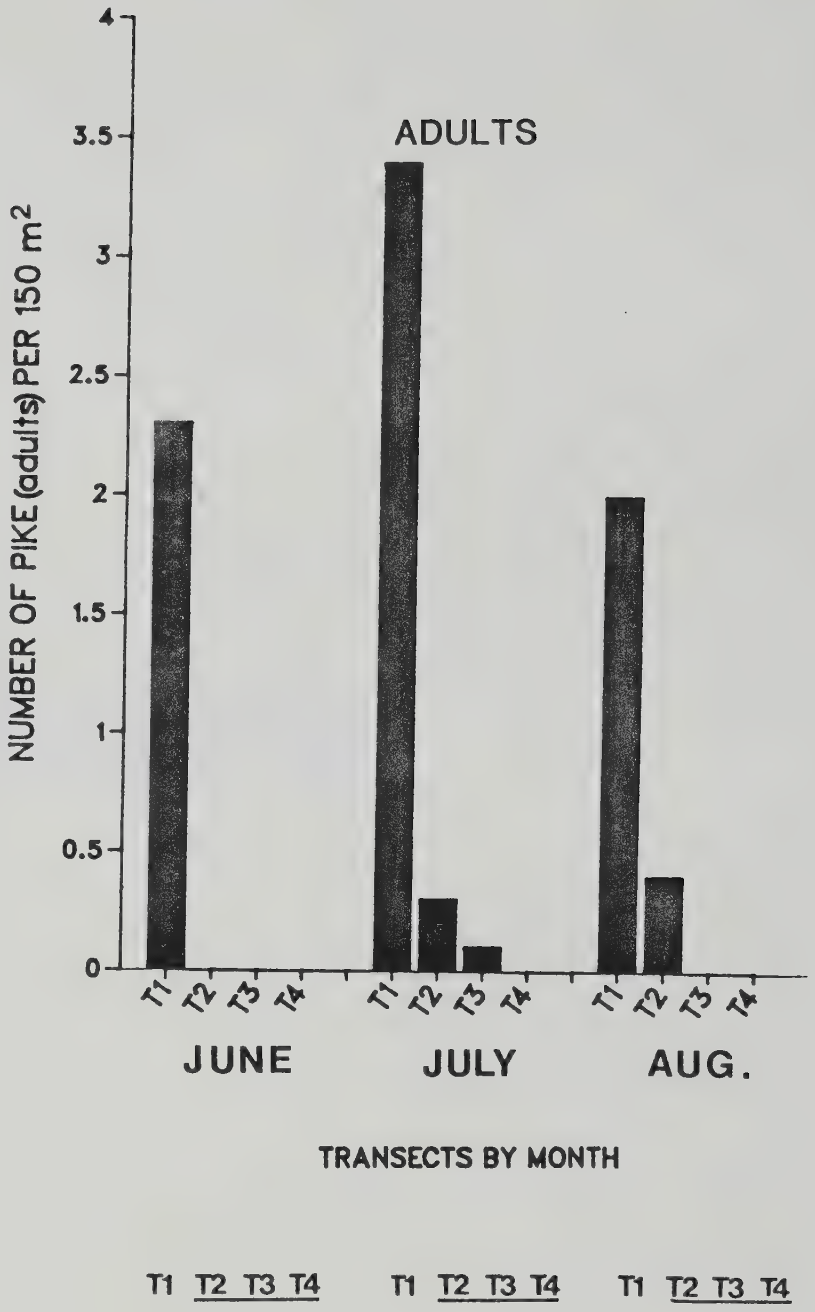

ADULTS
NUMBER OF PIKE (adults) PER 150 m2
0
0.5
1
1.5
2
2.5
3
3.5
4
T1
T2
T3
T4
JUNE
JULY
AUG.
TRANSECTS BY MONTH
T1 T2 T3 T4
T1 T2 T3 T4
T1 T2 T3 T4

Figure 2.4.

Percentage of juvenile and adult pike observed in each microhabitat category. The chi-square test was performed on the raw data (presented at the base of each bar); percentages have been used for graphic representation.

Ho: microhabitat use is independent of 'trophic' class

$X^2=7.81$, $df=2$, $0.025>P>0.01$

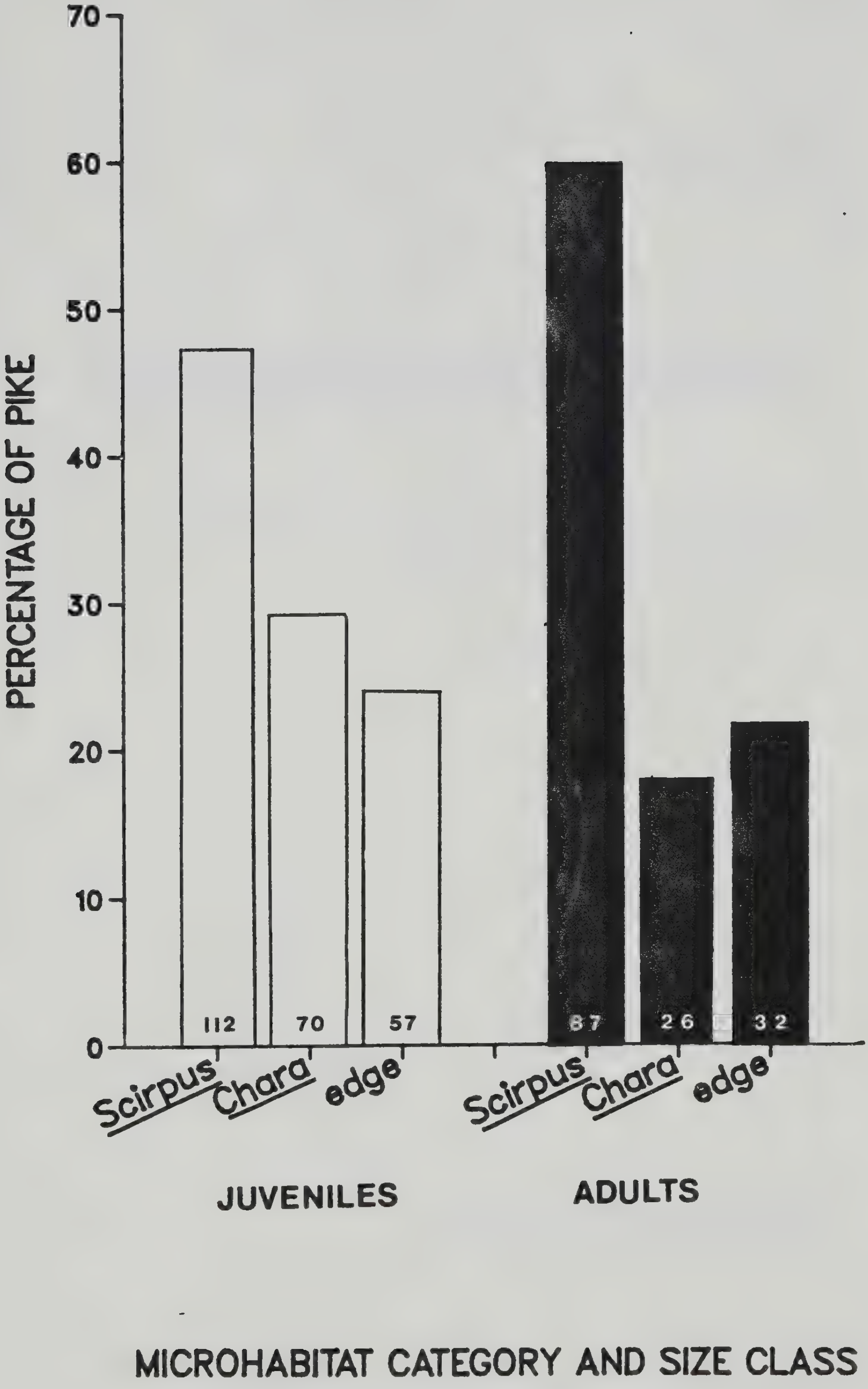
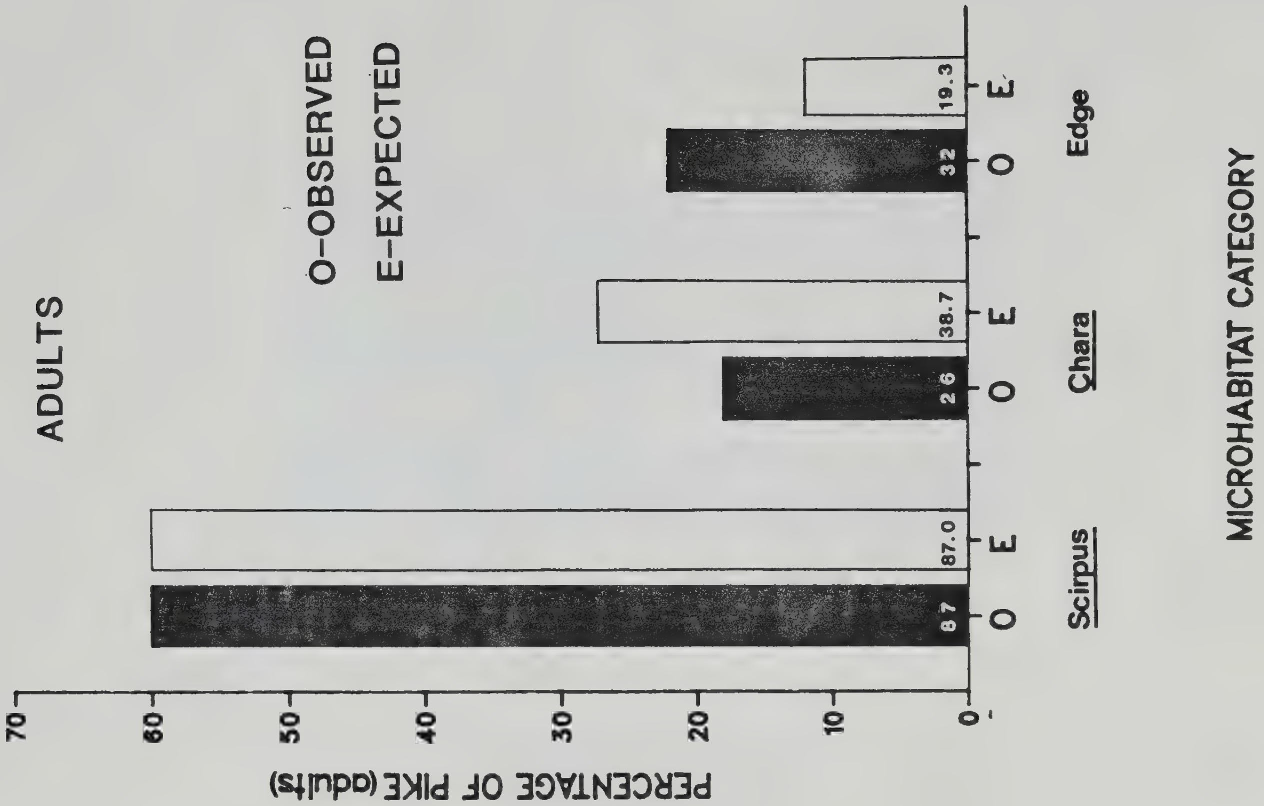

70
60
50
40
30
20
10
0
PERCENTAGE OF PIKE
112
70
57
87
26
32
Scirpus
Chara
edge
Scirpus
Chara
edge
JUVENILES
ADULTS
MICROHABITAT CATEGORY AND SIZE CLASS

Figure 2.5.

Percentage of adult and juvenile pike observed and expected in each microhabitat category. Chi-square tests were performed on the raw data (presented at the base of each bar); percentages have been used for graphic representations.

Ho: there is no significant difference between observed and expected microhabitat use

Juveniles: $X^2 = 27.45$, df=2, $P<0.005$
Adults: $X^2 = 12.53$, df=2, $P<0.005$


ADULTS
O-OBSERVED
E-EXPECTED
PERCENTAGE OF PIKE (adults)
0
10
20
30
40
50
60
70
87
87.0
26
38.7
32
19.3
O
E
O
E
O
E
Scirpus
Chara
Edge
MICROHABITAT CATEGORY

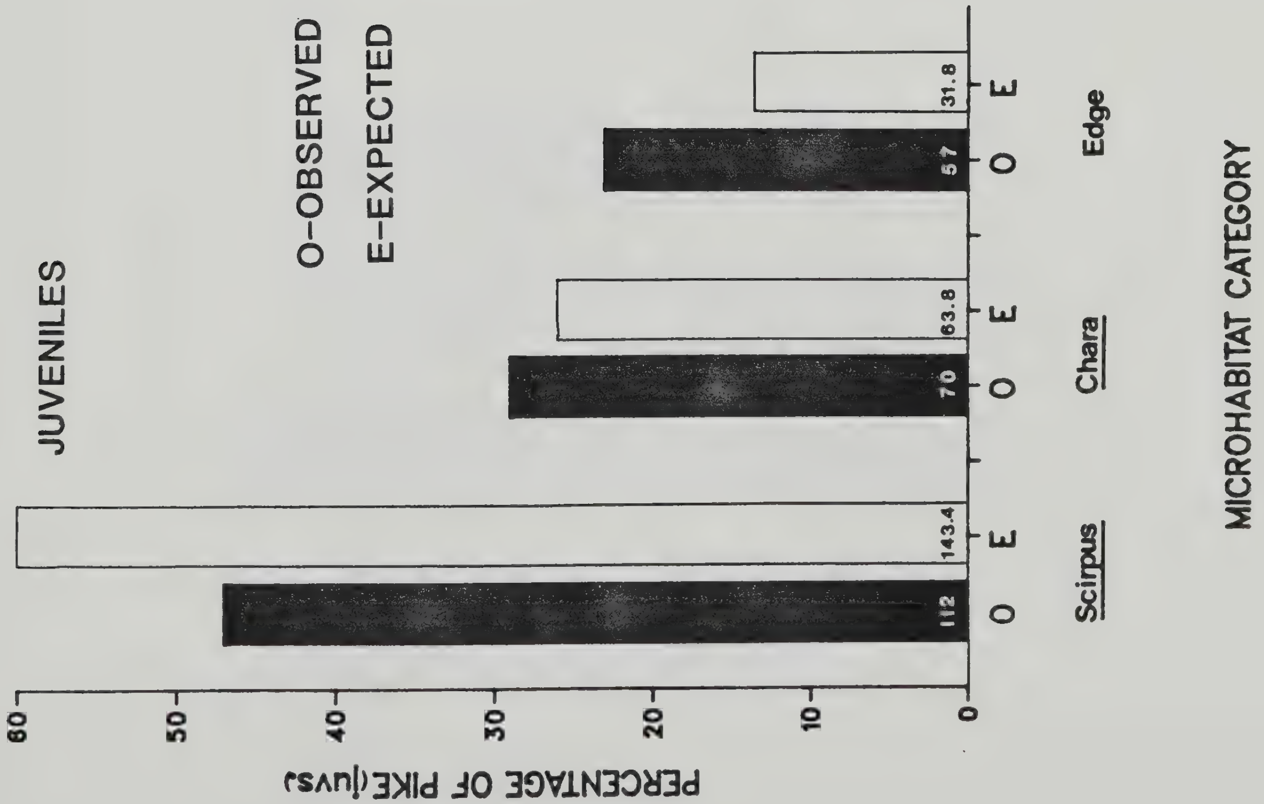
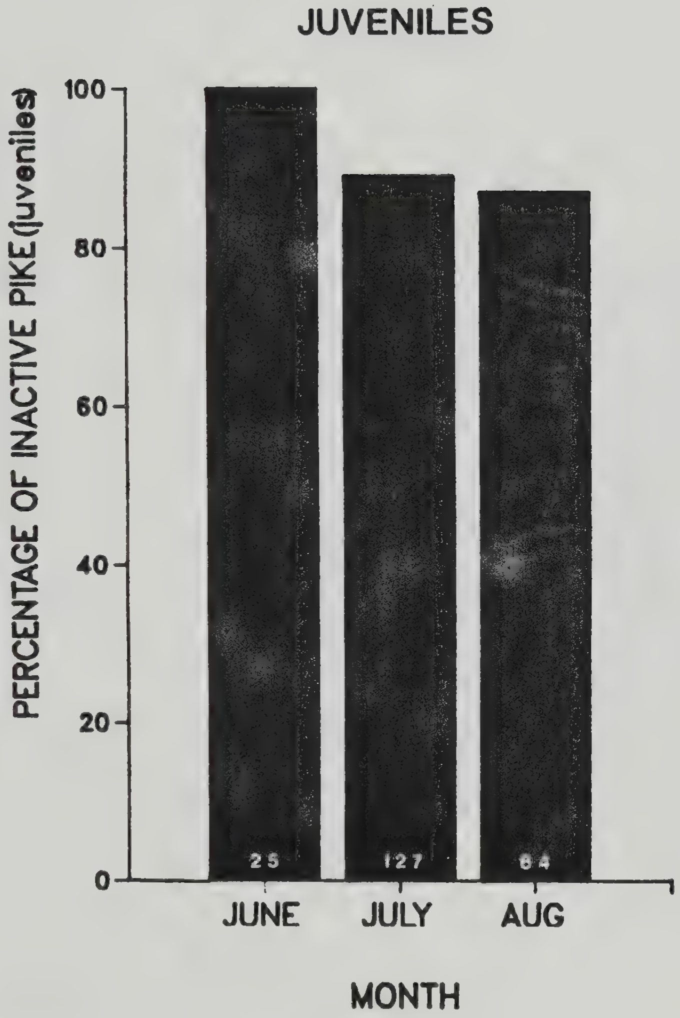

JUVENILES
O-OBSERVED
E-EXPECTED
PERCENTAGE OF PIKE (juvs.)
0
10
20
30
40
50
60
112
143.4
70
63.8
57
31.8
O
E
O
E
O
E
Scirpus
Chara
Edge
MICROHABITAT CATEGORY

Figure 2.6.

Percentage of inactive adult and juvenile pike observed in each month in Roi Lake. Chi-square tests were performed on the raw data (presented at the base of each bar); percentages have been used for graphic representations.

Ho: proportion of inactive pike is independent of month

Juveniles: $X^2=3.66$, df=2, $0.1>P>0.05$
Adults: $X^2=.02$, df=2, $P>0.975$


JUVENILES
PERCENTAGE OF INACTIVE PIKE (juveniles)
100
80
60
40
20
0
25
127
84
JUNE
JULY
AUG
MONTH

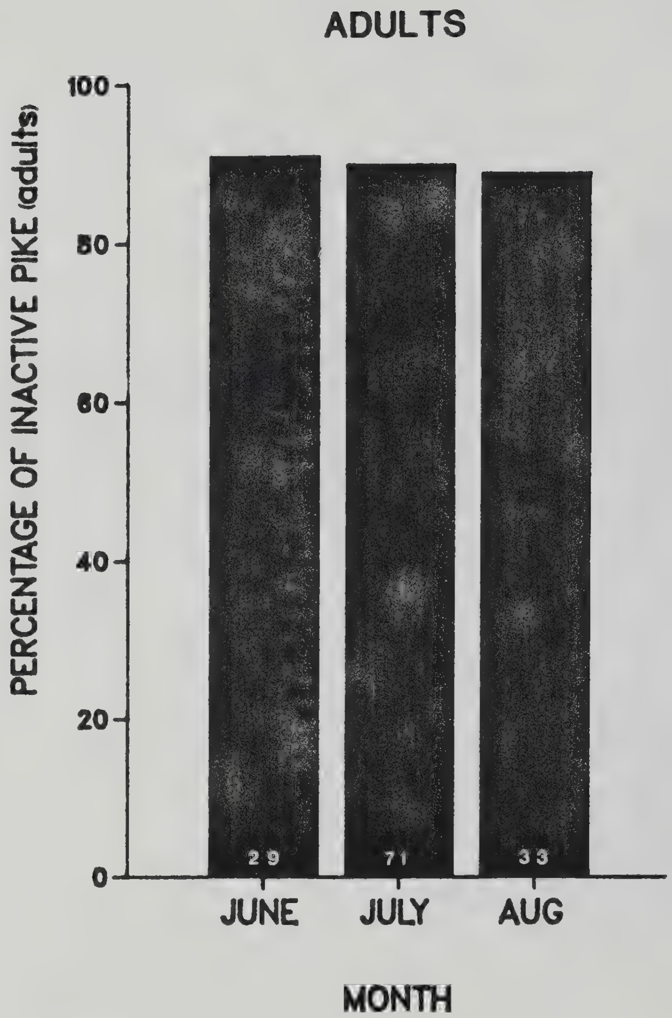
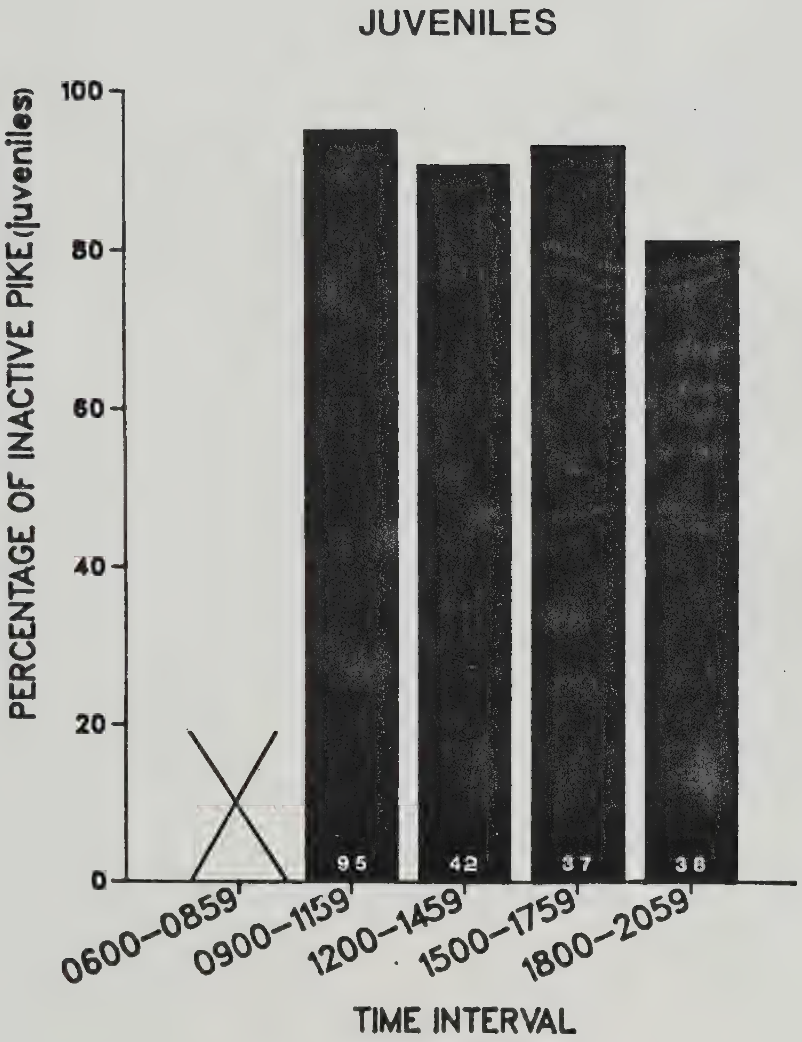

ADULTS
PERCENTAGE OF INACTIVE PIKE (adults)
100
80
60
40
20
0
29
71
33
JUNE
JULY
AUG
MONTH

Figure 2.7.

Percentage of inactive adult and juvenile pike in each time interval in Roi Lake. Chi-square tests were performed on the raw data (presented at the base of each bar); percentages have been used for graphic representations. The time periods marked with an 'X' represent intervals where the samples were not independent of the sample day and could not be pooled.

Ho: proportion of inactive pike is independent of time interval

Juveniles: $X^2=3.53$, df=3, $0.5>P>0.1$
Adults: $X^2=3.87$, df=3, $0.5>P>0.1$


JUVENILES
PERCENTAGE OF INACTIVE PIKE (juveniles)
100
80
60
40
20
0
95
42
37
38
0600–0859
0900–1159
1200–1459
1500–1759
1800–2059
TIME INTERVAL

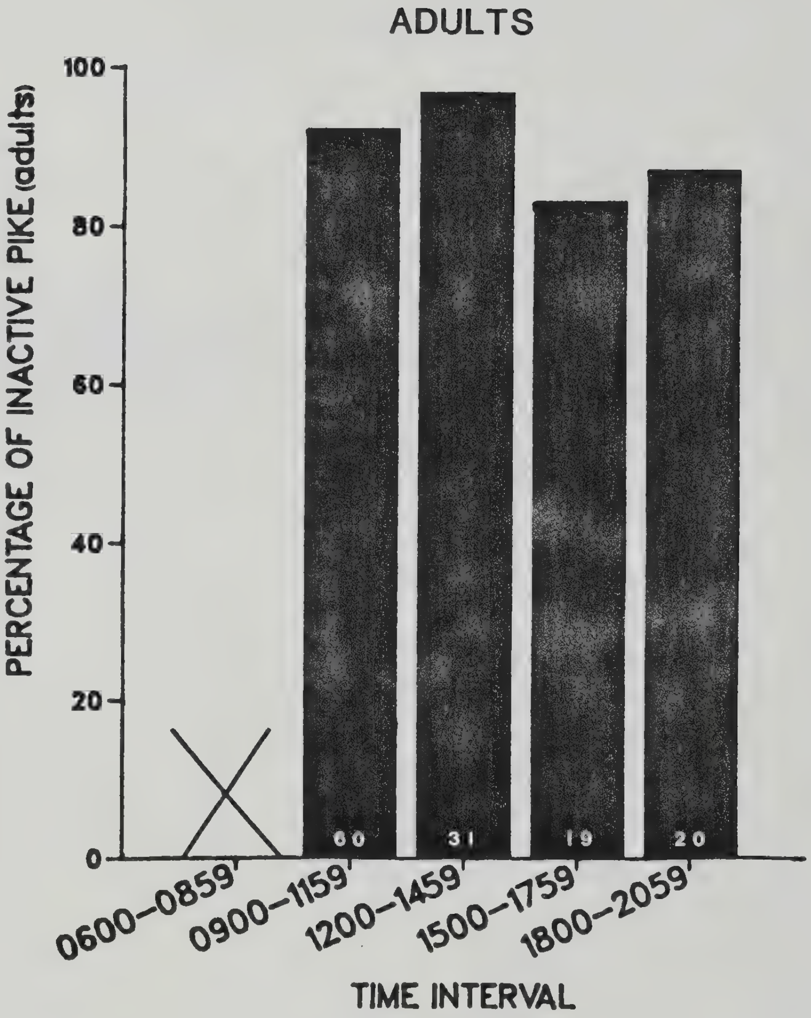

ADULTS
PERCENTAGE OF INACTIVE PIKE (adults)
100
80
60
40
20
0
60
31
19
20
0600–0859
0900–1159
1200–1459
1500–1759
1800–2059
TIME INTERVAL

Figure 2.8.

Number of pike observed on Transects 1, 5, and 6 during the summer months in Roi Lake. Data were analyzed using the Kruskal-Wallis test for differences between transects for each month and the Kruskal-Wallis multiple comparisons test for *a posteriori* comparisons between pairs of transects. Transect symbols underlined are not significantly different at $P<0.05$.

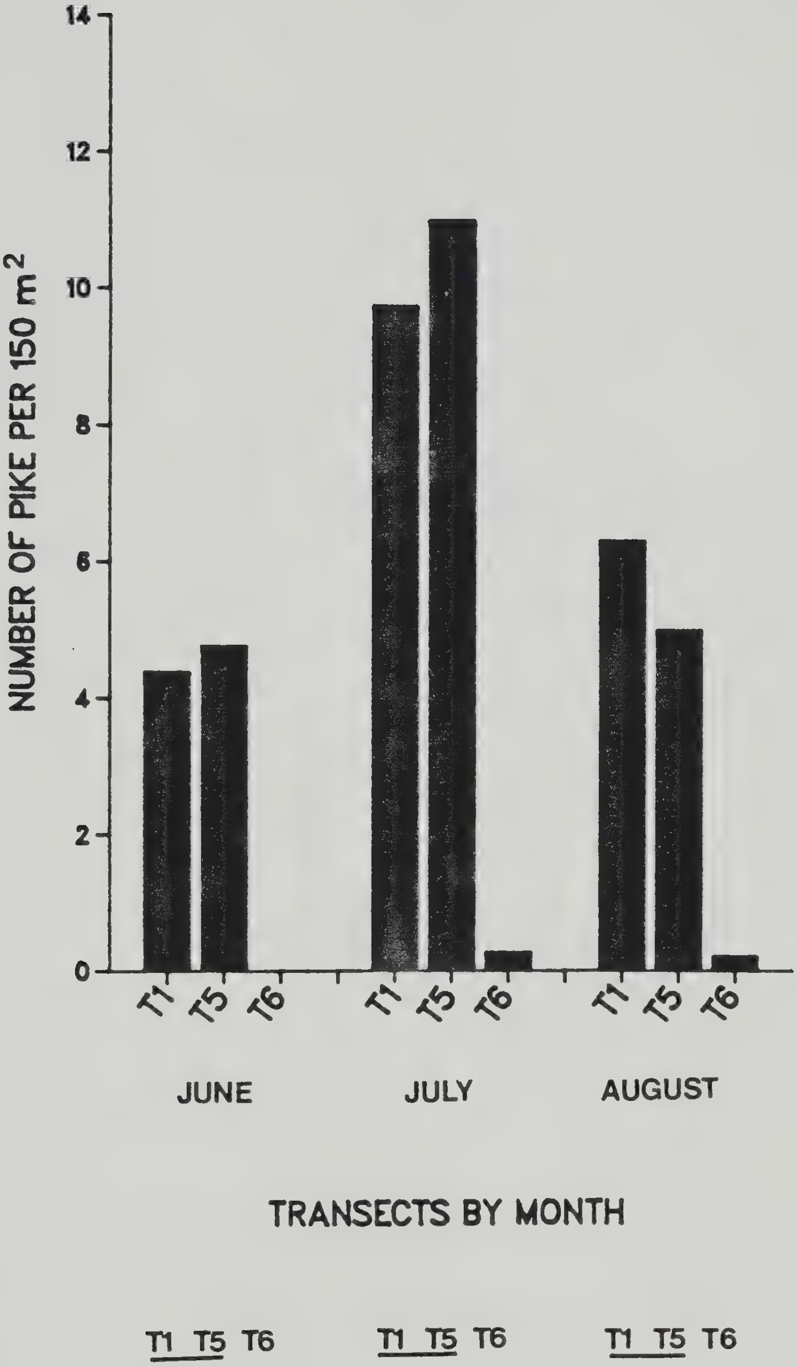

NUMBER OF PIKE PER 150 m^2
14
12
10
8
6
4
2
0
T1
T5
T6
T1
T5
T6
T1
T5
T6
JUNE
JULY
AUGUST
TRANSECTS BY MONTH
T1 T5 T6
T1 T5 T6
T1 T5 T6

Figure 2.9.

Frequency of occurrence of food items in the stomachs of juvenile and adult pike in Roi Lake during the summer months.

Juveniles: n=28
number of empty stomachs=15(54.0%)

Adults: n=44
number of empty stomachs=13(29.5%)

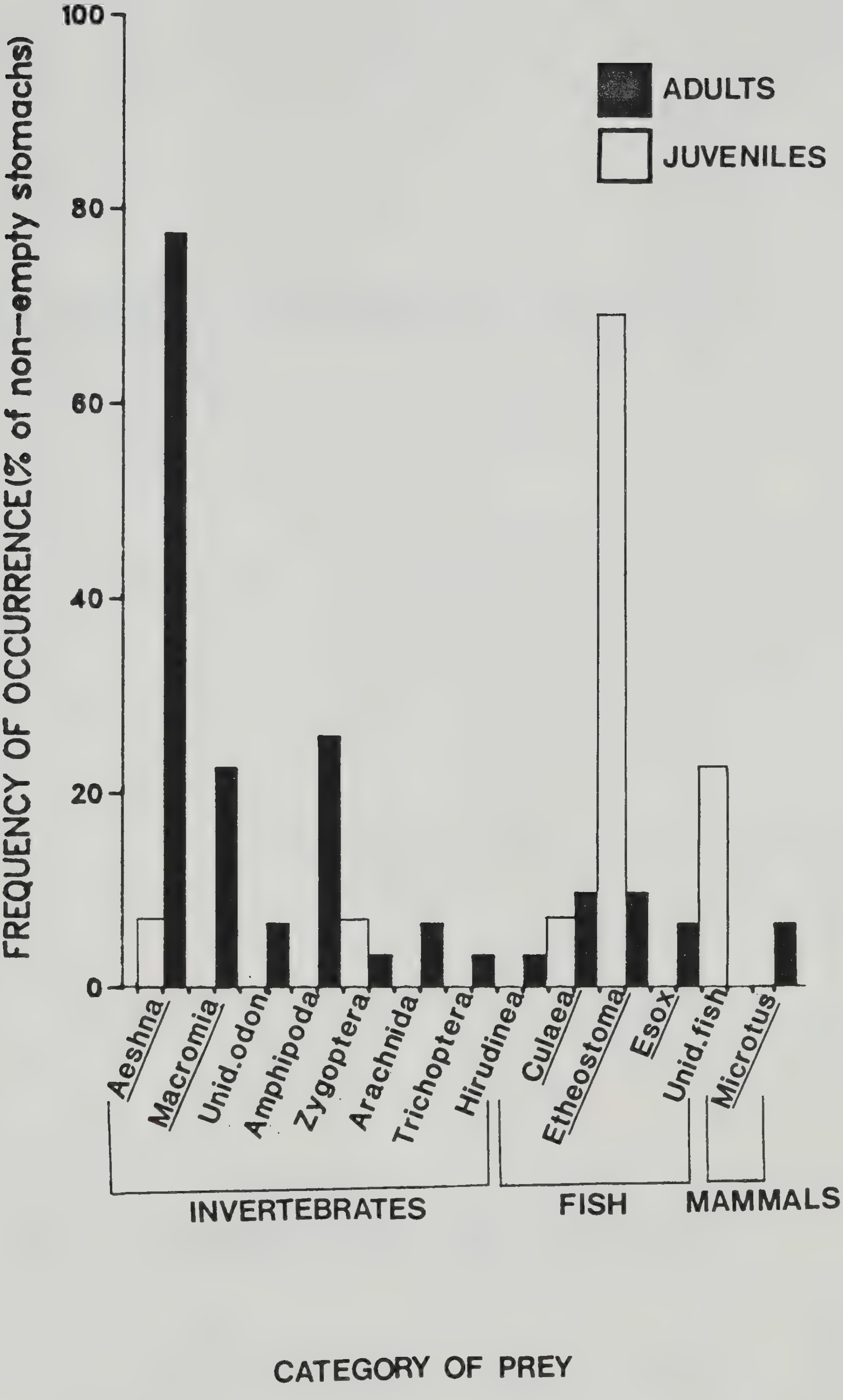

FREQUENCY OF OCCURRENCE(% of non-empty stomachs)
100
80
60
40
20
0
ADULTS
JUVENILES
Aeshna
Macromia
Unid.odon
Amphipoda
Zygoptera
Arachnida
Trichoptera
Hirudinea
Culaea
Etheostoma
Esox
Unid.fish
Microtus
INVERTEBRATES
FISH
MAMMALS
CATEGORY OF PREY

Figure 2.10.

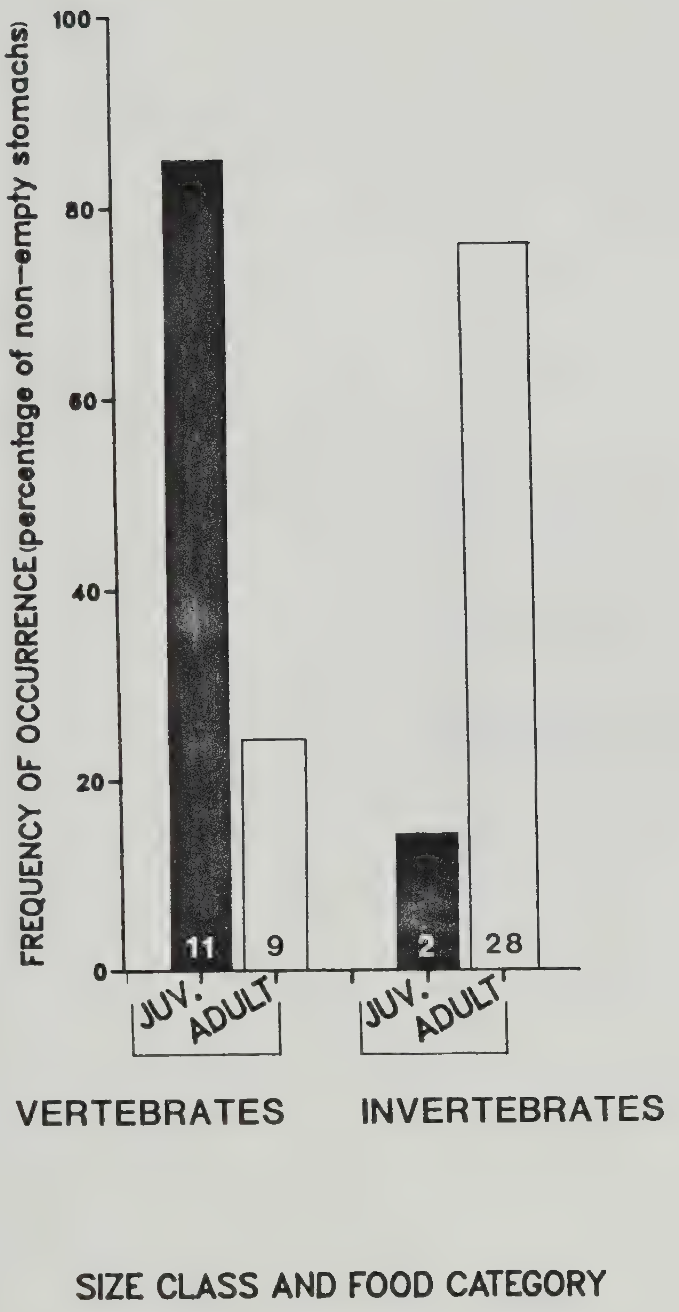
Stomach contents of juvenile and adult pike in Roi Lake during the summer months: frequency of occurrence and percentage composition by number of individual items in each food category. Chi-square tests were performed on the raw data (presented at the base of each bar); percentages have been use for graphic representations.

Ho : frequency of occurrence of food category is independent of size class (J vs A)

$X^2=12.17$, df=1, $P<0.005$

Ho : percentage composition by number of items in each food category is independent of size class (J vs A)

$X^2=65.26$, df=1, $P<0.005$


FREQUENCY OF OCCURRENCE (percentage of non-empty stomachs)
100
80
60
40
20
0
11
9
2
28
JUV.
ADULT
JUV.
ADULT
VERTEBRATES
INVERTEBRATES
SIZE CLASS AND FOOD CATEGORY

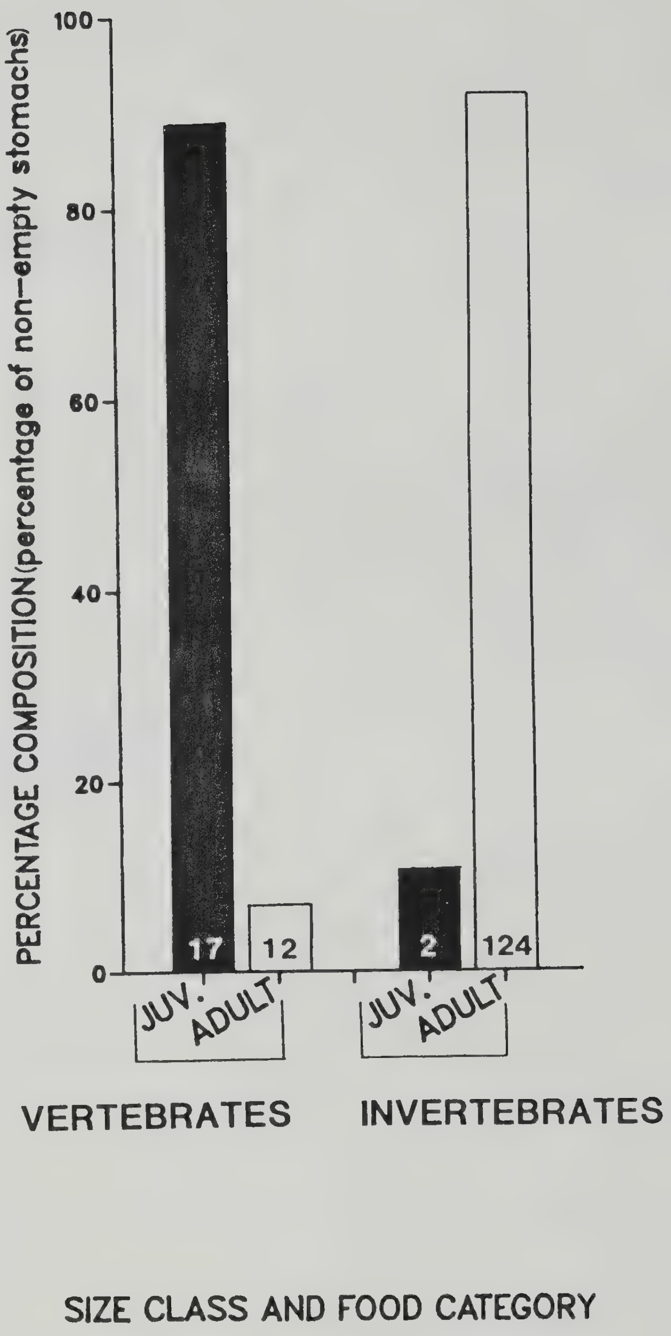

PERCENTAGE COMPOSITION (percentage of non-empty stomachs)
100
80
60
40
20
0
17
12
2
124
JUV.
ADULT
JUV.
ADULT
VERTEBRATES
INVERTEBRATES
SIZE CLASS AND FOOD CATEGORY

Figure 2.11.

Microhabitat use by dragonfly nymphs in Roi Lake in less than 2 metres of water (n=46).

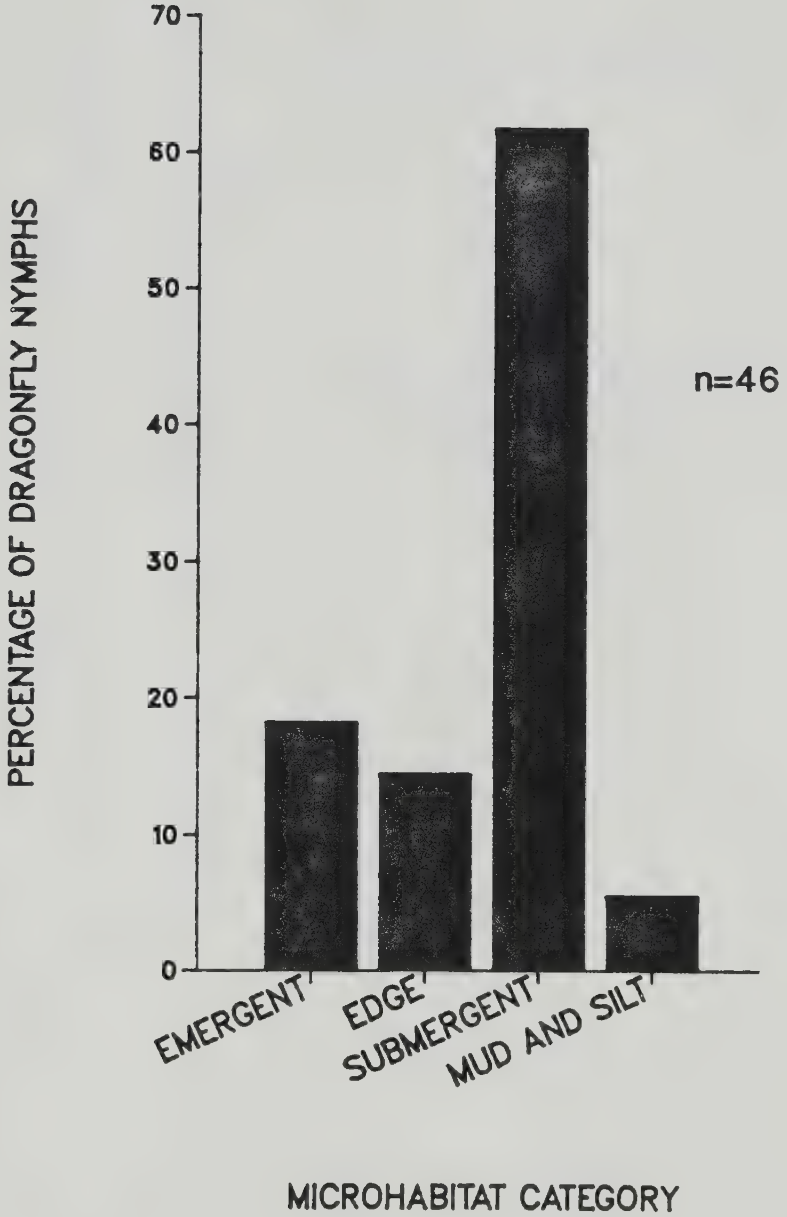

70
60
50
40
30
20
10
0
PERCENTAGE OF DRAGONFLY NYMPHS
n=46
EMERGENT
EDGE
SUBMERGENT
MUD AND SILT
MICROHABITAT CATEGORY

Figure 2.12.

Relative abundance of juvenile Iowa darters versus juvenile pike in Roi Lake during the summer months. There was no relationship between the relative abundance of juvenile Iowa darters and juvenile pike on Transects 1 to 6 (Spearman correlation, P=0.479).

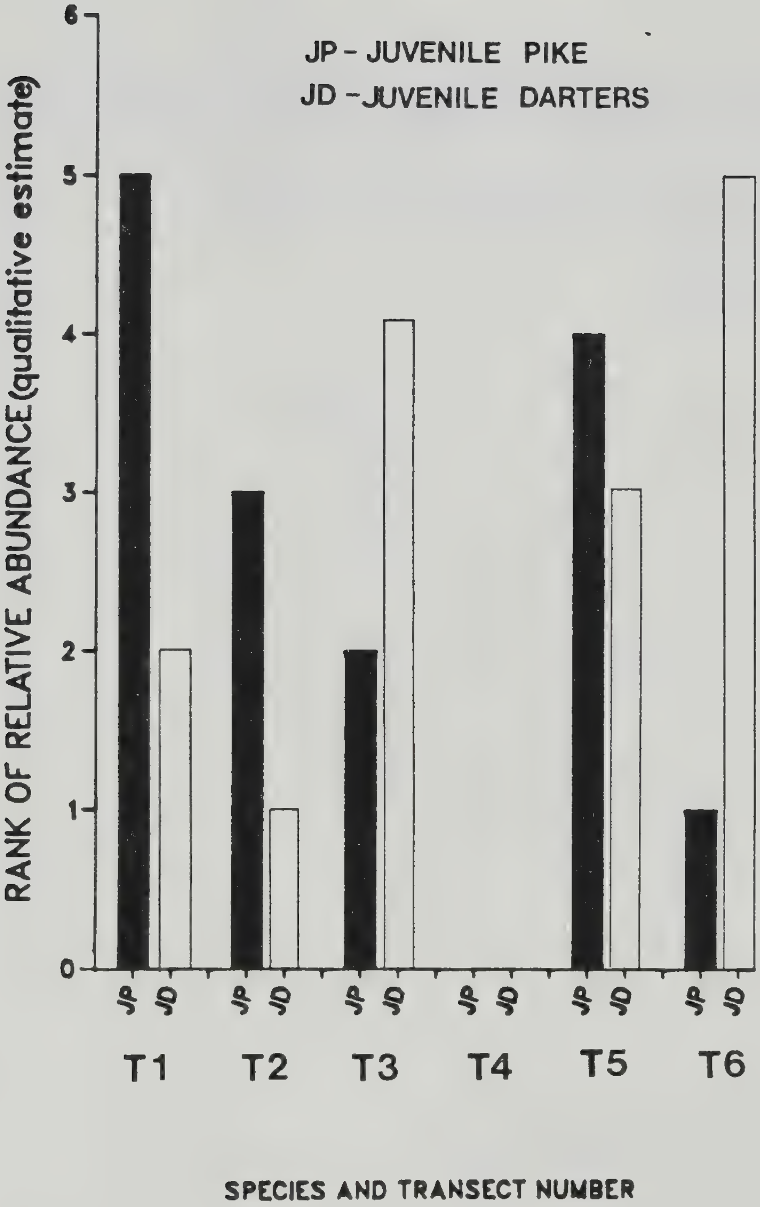

JP - JUVENILE PIKE
JD - JUVENILE DARTERS
RANK OF RELATIVE ABUNDANCE (qualitative estimate)
0
1
2
3
4
5
6
JP
JD
T1
T2
T3
T4
T5
T6
SPECIES AND TRANSECT NUMBER

Figure 2.13.

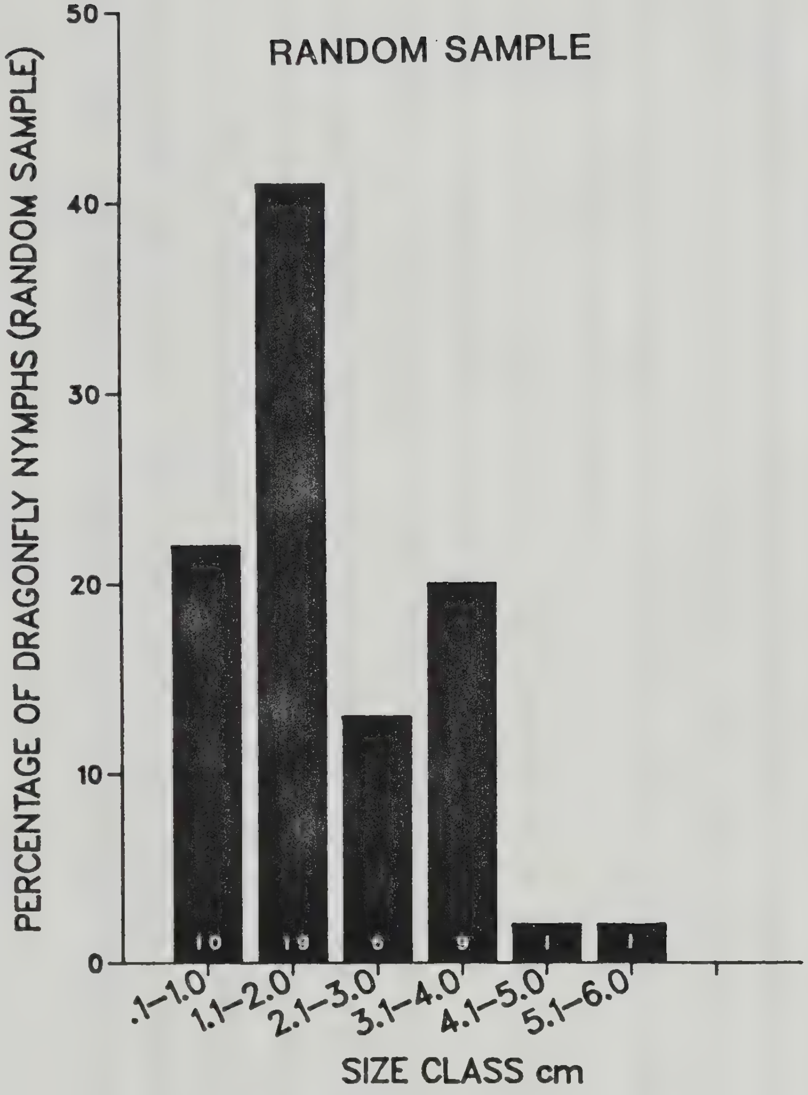
Size frequency histogram of anisopterans (dragonfly nymphs) eaten by pike and randomly collected in Roi Lake.

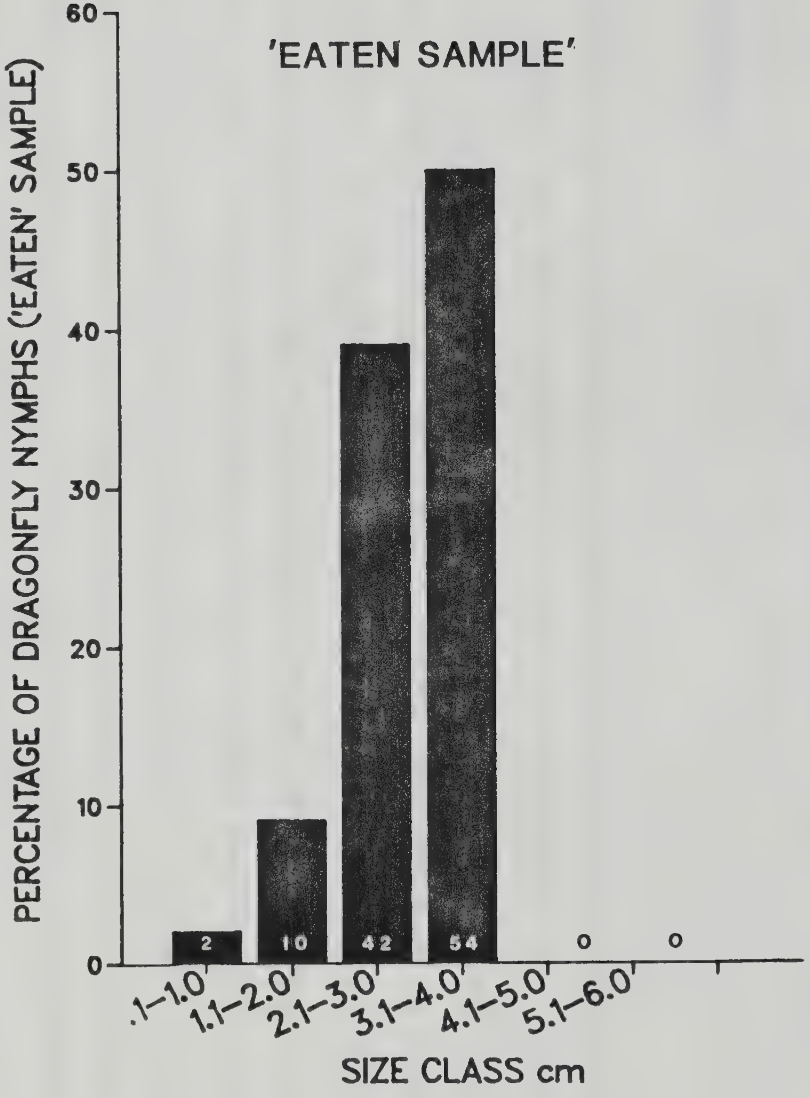
A) random sample B) 'eaten'sample ie. nymphs consumed by pike

The chi-square test was performed on the raw data; percentages have been used for graphic representations. The numbers of consumed and visually collected nymphs in each size class are presented at the base of each bar.

Ho: there is no significant difference between the observed ('eaten') sample and the expected (random) sample

$X^2=122.58$, $df=4$, $P<0.001$


RANDOM SAMPLE
PERCENTAGE OF DRAGONFLY NYMPHS (RANDOM SAMPLE)
0
10
20
30
40
50
10
19
6
9
1
1
.1–1.0
1.1–2.0
2.1–3.0
3.1–4.0
4.1–5.0
5.1–6.0
SIZE CLASS cm


'EATEN SAMPLE'
PERCENTAGE OF DRAGONFLY NYMPHS ('EATEN' SAMPLE)
0
10
20
30
40
50
60
2
10
42
54
0
0
.1–1.0
1.1–2.0
2.1–3.0
3.1–4.0
4.1–5.0
5.1–6.0
SIZE CLASS cm

III. SPATIAL RESOURCE USE AND A SEASONAL TROPHIC SHIFT IN THE NORTHERN PIKE OF MERE LAKE, ALBERTA

A. INTRODUCTION

Temperate fish have evolved in an unpredictable environment characterized by longterm glaciation and under conditions of varying species diversity and community composition. In addition, the seasonal nature of the temperate lake is reflected in marked fluctuations in the abundance and distribution of critical resources such as food and vegetation cover. A seasonally dynamic resource base may significantly alter the ecological interactions among species, in particular, predator-prey relationships. Such an evolutionary history and the dynamic nature of the temperate lake would favour less specialization of fish species than in predictable, stable environments (Emery 1973, Hall and Werner 1977, Helfman 1979). The ability of a species to use different habitats to exploit peak prey abundances or to modify diet in response to changes in the availability of prey species within a restricted habitat must be important to the success of these species.

Plasticity in foraging strategy is reflected in the monthly shifts in diet exhibited by a number of temperate fish species including perch, bluegill, brown trout, char, minnows, killifish, rock bass, largemouth bass, and mudminnows (Frost 1954, Keast 1970, Keast 1977). Seasonal dietary shifts in more specialized feeders tend to be limited to changes in the proportions of the kinds of prey consumed; while in more generalized feeders, items of high consumption frequency in one month may in the next month be completely absent or relatively insignificant (Keast 1970).

One would predict that these seasonal trophic shifts would be related to seasonal or monthly shifts in depth distribution, microhabitat use, and foraging rate.

The northern pike (Esox lucius) is a top predator in many freshwater ecosystems of the north-temperate region. Pike are very plastic with respect to foraging strategies exhibiting age- or size-related trophic shifts (Hunt and Carbine 1950, Franklin and Smith 1963, Munro 1957, Bregazzi and Kennedy 1980, Mann 1982), seasonal dietary shifts (Frost 1954, Lawler 1965, Mann 1982, Mackay unpubl. data) and major geographic differences in diet. Pike are generally considered to be piscivorous; and seasonal dietary

change usually involves a shift in the fish species eaten, proportions of fish species consumed, or the size class used within a prey species (Frost 1954, Lawler 1965, Christiansen 1976, Diana 1979a, Bregazzi and Kennedy 1980, Koz'min 1981). However, in some northern pike populations, seasonal shifts may involve major changes in prey type (invertebrates--fish) (Christiansen 1976, Mackay unpubl. data).

Although the existence of seasonal dietary change has been well documented in a number of pike populations, there are few studies which have examined the relationships between these major trophic shifts and the foraging rates and distribution patterns in this species.

The objective of the present study was to assess the factors affecting the distribution pattern and foraging rate of northern pike in a free-living population. I hypothesized that a seasonal trophic shift would be reflected in a change in the distribution pattern and foraging rate of the pike population. Foraging rate was defined as the intake of prey items per unit of time. In addressing this hypothesis, I will first describe the distribution pattern, measured directly, and foraging rate, measured indirectly, of the northern pike and then relate both distribution and foraging rate to various factors which may affect these niche dimensions. The major factor evaluated was a seasonal trophic shift. In addition, various abiotic factors and aquatic macrophyte distribution were examined. This approach allows one to assess the relative importance of prey use as a factor influencing the rate of foraging activity and the distribution pattern of the pike population. The investigation was limited to the summer months, the period of the year in which 60 percent of the total annual ration is consumed and feeding frequencies are relatively high (Diana 1979a).

B. MATERIALS AND METHODS

Study Site

The research was conducted during early May to late August of 1983 on Mere Lake, Alberta (53°51'N, 114°03'W), a relatively deep, mesotrophic water body located 40 kilometres northwest of Edmonton, Alberta. The lake (59 hectares in surface area, Rhude 1979) consists of five basins with maximum basin depth ranging from 9 to 17 metres

(Figure 3.1). The shoreline has remained largely undeveloped with limited public access. Mere Lake was characterized by an extensive littoral zone and a diverse macrophyte flora. The zone of emergent vegetation was dominated primarily by Typha and Sparganium with patches of Equisetum, Sagittaria, and Potamogeton natans. Areas deeper than 0.8 metres in depth were dominated by Chara, Ceratophyllum, Myriophyllum, Potamogeton with patch areas of Ranunculus and Najas. The emergent macrophyte zone extended as far as 20 metres from the shore to a depth of 0.8 metres; the zone of submergent vegetation extended as far as 200 metres from shore to a depth of 5 metres. The lake was thermally stratified during the summer months with the metalimnion commencing at a depth of 2-5 metres, and was characterized by a clinograde oxygen profile with the chemocline commencing at a depth of 4 metres.

Mere Lake supports populations of northern pike (Esox lucius) and yellow perch (Perca flavescens).

Descriptive Analyses - Depth Distribution and Microhabitat of Northern Pike

As a preliminary survey of the distribution of northern pike in Mere Lake, randomly selected areas of the lake were censused by snorkel and SCUBA (self-contained underwater breathing apparatus) in the last 3 weeks of May, 1983. Results of this survey indicated that 85 percent of the observed pike were associated with vegetation in less than 1.0 metres of water.

Based on the results of the preliminary census, a stratified sampling regime was used to assess changes in the distribution of northern pike on a monthly basis. Basin I (Figure 3.1) was selected as the study site, and transect lines of yellow polypropylene rope (marked off at 1 metre intervals and 100 to 200 metres in length) were placed at seven different depths from 0.4 to 4.6 metres, in representative habitat areas. Transect location, depth, and vegetation charateristics are presented in Figure 3.2 and Table 3.1. The average Secchi disk reading was 4.0±1.0 m (standard deviation, n=9, Appendix II, Table 1) during June, July, and August. Based on clarity of the water, and approachability and crypticity of northern pike, a 3 metre strip width was considered to be optimal.

To examine month to month variation in the distribution of northern pike, transects were surveyed using snorkel and SCUBA during the daylight hours in the last 3 weeks of

June, July, and August, an average of four times per month (daylight hours were defined as the hours of the day between the end of nautical sunrise and the beginning of nautical sunset, determined from the Nautical Almanac (Anonymous 1981), correcting for longitude and latitude). In addition, approximately 100 transects were surveyed across the limnetic areas at various depths in all five basins throughout the entirety of the sampling period. No pike were seen in the offshore limnetic waters.

To examine habitat use and habitat selection on a finer scale than depth, the microhabitat used by each pike observed on Transects 1 and 2 was recorded. These were the transects in which pike abundance was the highest. Microhabitats were defined as areas at a given depth differentiated by vegetation characteristics. A fish was considered to be 'in' a specified microhabitat category if more than one half of its body length was within the area.

A systematic sampling regime was used to address the question; is the littoral distribution of northern pike observed in the Basin I study area representative of the entire lake? Sampling of the population was restricted to the peripheral zone of the lake less than 2.5 metres in depth. The shoreline was marked off into 200 metre intervals dividing the littoral area into 30 zones of equal width. An additional zone was sampled in the littoral area dividing Basin I and Basin II (Figure 3.1). Zones were divided into three morphometric regions for census: Area A which was <0.5 metres in depth, Area B which was 0.5 to 1.5 metres in depth, and Area C which was 1.5 to 2.5 metres in depth. Approximately every third zone and all areas within the zones were visually censused on a monthly basis using an estimated 3 metre strip width.

All underwater observation data were recorded on pre-coded waterproof plastic paper. In addition to information concerning microhabitat and depth distribution, the total length of each pike sighted was estimated. The accuracy of the estimate was determined by comparing the estimated total length of each of 10 tagged pike to the recorded total lengths of these individuals measured to 0.1 centimetres.

It is well documented in the literature that pike are primarily visual predators (Solman 1945, Hoogland et al. 1956, Nursall 1973, Christiansen 1976), relatively inactive at night (Malinin 1969, 1970, Diana 1980, Mackay unpubl.), and in general, diurnal with respect for foraging activities (Solmon 1945, Lagler 1956, Kamyshnaya and Tsepkin

1973). Although crepuscular periods are often favored for foraging activities by top predators (Hobson 1972 1974) temperate predators do not exhibit visual specialization for predatory activities during the twilight periods of rapidly changing levels of light intensity with the exception of the walleye (Helfman 1979). Thus, it was assumed in the present investigation that changes in distribution and microhabitat use by northern pike as related to seasonal prey use characteristics would be detected by limiting observations to the daylight hours justified by the diurnal nature of northern pike and the related visual mode of feeding.

Strengths and limitations of the underwater census technique in the study of northern pike have been previously described for the pike population of Roi Lake, a similar small lake near Mere Lake (Chapter I). A tagging study on the Roi Lake population was used to validate the assumption of independence i.e. that the same individuals were not observed on subsequent sample days. In the present investigation, chi-square analyses indicated that microhabitat use was independent of day for each month. Results were thus pooled on a monthly basis for these homogeneous samples.

Depth distribution data were analyzed using a Kruskal-Wallis test, a nonparametric analogue of a single classifaction analysis of variance. A posteriori comparisons between pairs of transects were tested using a Kruskal-Wallis multiple comparisons test (Sokal and Rohlf 1969, Conover 1980). Corrections were made for tied observations. Chi-square analysis was used to test for independence of microhabitat use with respect to month. The chi-square test for goodness of fit was used in the analysis of microhabitat selection. Values were considered to be significantly different at $P<0.05$. Standard deviations (S.D.) are presented where estimates of the amount of variation are given for mean values.

Environmental Factors

To examine the relationships between abiotic factors and the distribution and foraging rates of pike in Mere Lake, dissolved oxygen concentration and water temperature were monitored throughout the summer months using standard limnological procedures. Water level was recorded from May 24 to August 27, 1983.

Profiles of dissolved oxygen concentration, measured using a modified Winkler technique (Carpenter 1965), and water temperature, measured using a

Montedoro-Whitney thermistor, were collected on a monthly basis (May to August) at 2 metre intervals in all five basins. In addition, temperature profiles were collected ten times throughout the period of investigation at 1 metre intervals in all basins.

Biotic Interactive Factors

To ensure a representative sample of the northern pike in Mere Lake, 156 pike were aquired using three different techniques: fly-fishing, spin-casting with lures (spoons and plugs), and spear-fishing. Food habits were examined by flushing out the stomachs of pike using a modified version of the stomach pump described by Crossman and Hamilton (1978). Pike were anaesthetized with M.S.222 (tricaine methane sulfonate).

Stomach contents were preserved in 10 percent formalin pending laboratory analysis. Contents were identified, and the length of each item was measured or estimated when digestion precluded an accurate length measurement.

Chi-square analysis was used to test whether diet composition was independent of month with respect to major food types eaten.

The percentage of empty stomachs, the mean number of prey items per fish, and the mean size of prey item per fish were determined. The rate of foraging activity was evaluated indirectly through interpretation of these results. Data were analyzed using the Mann-Whitney U test for differences in mean prey size per fish and a t-test for differences in the mean number of items per fish (log transformed data) on a seasonal basis. A Pearson correlation was used to test for a significant relationship between predator size and prey size, and predator size and number of items consumed (Sokal and Rohlf 1973).

The distribution and habitat use of the two major invertebrate prey types, anisopterans and amphipods, were examined through the collection of Ekman dredge samples using a stratified systematic sampling regime. It has been reported in the literature (Makowecki 1973, Keast and Harker 1977a) that invertebrate biomass is biased significantly towards the littoral zone. Based on the assumption that a large proportion of the amphipod and anisopteran populations occur in the shallower areas, the lake was divided into two strata: the 0 to 3 metre stratum which was sampled intensively and the greater than 3 metre stratum in which the number of samples was relatively small.

Duplicate dredge samples were taken at four depths (<0.5 metres, 1, 2, and 3 metres) in each of 10 peripheral zones as designated in the systematic littoral survey of the pike population (Figure 3.1). In addition, duplicate samples were taken at 5, 7, 9, 11, 13, and 15 metres in Basin I. The sampling regime was replicated in July and August producing a total of 202 dredge samples. Samples were examined for anisopterans and amphipods (greater than 4 mm in length). The 4 millimetre length criterion was chosen, as prey items less than 4 millimetres in length were not used by adult pike in Mere Lake.

In addition, a sample of dragonfly nymphs was collected in less than 1.5 metres of water within the study basin. All major habitat categories were represented in this depth stratum. Nymphs were collected by snorkelling in randomly selected zones; and thus the sample obtained reflects those anisopterans which could be located visually.

The Wilcoxon signed-ranks test was used to test for differences between duplicate samples for anisopterans and amphipods in both July and August (Sokal and Rohlf 1973). Depth distribution data were analyzed using the Mann-Whitney U test for directional differences between the two strata and the Kruskal-Wallis test for differences within each stratum. The Kruskal-Wallis multiple comparisons method was used to carry out a posteriori comparisons between individual depths within the 0 to 3 metre stratum (Sokal and Rohlf 1969, Conover 1980). Differences in total numbers of amphipods and anisopterans between months were examined using the Mann-Whitney U test. Chi-square analysis was used to test for association between habitat use and month for both anisopterans and amphipods taken in Ekman dredge samples, and association between the habitat use by anisopterans from Ekman dredge samples and anisopterans from the visually collected random sample. The total length of amphipods and anisopterans was recorded to the nearest millimetre. A t-test was used to test for a significant difference between the mean size of consumed anisopterans and the mean size of anisopterans available in the environment as determined from analysis of Ekman dredge samples (log transformed data). The Mann-Whitney U test was used for a similar analysis on the consumed amphipods and those collected in Ekman dredge samples.

The distribution of yellow perch (Perca flavescens) was assessed using the systematic sampling survey of the littoral area as outlined for the broadscale survey of northern pike. The number of perch 'sightings' was recorded monthly by census of the

11 selected zones. Perch tend to travel as individuals, aggregations, or schools; thus, one 'sighting' was considered to be one individual, one aggregation, or one school. This technique allows one to assess changes in distribution patterns but does not provide information with respect actual numbers of perch.

Perch distribution data were analyzed using the Kruskal-Wallis test for differences between the 3 months in each morphometric area and the Kruskal-Wallis multiple comparisons test for a posteriori comparisons between months (Sokal and Rohlf 1969, Conover 1980).

C. RESULTS

Distribution Patterns

Northern pike were observed approximately 237 times in the month by month examination of depth distribution patterns and microhabitat use within the Basin I study area. The mean total length (estimated to within ± 5 cm) of the pike observed was 35.2± 15.5 centimetres (S.D., n=237, range=16-99 cm).

The distribution of adult northern pike in relation to lake morphometry suggests selective use of shallow, vegetated habitat by pike in Mere Lake (Figure 3.3). There were significantly more adult pike on Transects 1 and 2 than on Transects 3 to 7 during June, July, and August (Kruskal-Wallis tests, $P<0.05$).

Use of shallow habitat by northern pike in Mere Lake is further supported by results of the systematic survey in which the littoral area of all five basins was censused. A total of 193 pike were observed in the systematic survey during June, July, and August; and there were significantly more adult pike observed in Area A (<0.5 m) than in Area B (0.5-1.5 m) or Area C (1.5-2.5 m) (Kruskal-Wallis tests, $P<0.05$, Figure 3.4). Thus, the depth distribution of adult pike observed in the study area appears to represent the depth distribution of the entire population.

Microhabitat use was examined for pike observed on Transects 1 and 2, the transects with the highest abundance of northern pike. The microhabitat most heavily used by pike on both Transects 1 and 2 was the area of emergent vegetation (Figure 3.5). There were no significant differences in microhabitat use between months on either

Transect 1 (X^2=6.88, df=4, 0.25>P>0.1, Figure 3.5) or Transect 2 (X^2=4.99, df=4, 0.5>P>0.25, Figure 3.5).

An examination of microhabitat selection, rather than microhabitat use demands a comparison of the observed habitat use and the expected habitat use based on the proportion of available habitat in each microhabitat category. There was a significant difference between the observed and expected results for both Transect 1 (X^2=57.23, df=2, P<0.005, Figure 3.6) and Transect 2 (X^2=17.79, df=2, P<0.005, Figure 3.6). On Transect 1, northern pike were associated with deadfall (dead trees and branches) and emergent vegetation more than would be expected by chance and observed in areas of submergent vegetation less than would be expected by chance. On Transect 2, again, pike were observed in areas of emergent vegetation more than would be expected by chance.

Environmental Factors

Mere Lake showed relatively small fluctuations in water level presumably due to connections with groundwater aquifers. The maximum recorded change in water level between May 24 and August 27, 1983 was 12 centimetres; and this factor was thus considered to have had no appreciable influence on the distribution of pike during the period of investigation (Appendix II, Figure 1).

Temperature profiles indicate that Mere Lake was thermally stratified during late May, June, July, and August with the metalimnion commencing at a depth of 2 metres in May, and 3-5 metres in June, July, and August (Table 3.2, Appendix II, Table 2).

A consideration of temperature data in light of the descriptive analyses of pike distribution in Mere Lake indicates that in all basins, pike were most abundant in the warmest depth stratum during the daylight hours.

During June, July, and August, dissolved oxygen concentration dropped markedly in the 4-6 metre depth stratum from levels at or above saturation to less than 4 mg/L. Interbasin variability in dissolved oxygen concentration was low in June, July, and August (Table 3.2).

The distribution of adult northern pike in the Mere Lake study area was restricted to a depth stratum characterized by saturated oxygen during the daylight hours.

Biotic Interactions

Prey Use

The stomach contents of 156 northern pike were examined (mean total length = 44.6±10.5 cm, S.D., n=156, range=16-58 cm). Prey use was examined by calculating the percentage of pike stomachs sampled containing each category of food item, expressed as a percentage of all non-empty stomachs for the months of May through August inclusive (Figure 3.7). During May, June, and July, adult pike fed almost exclusively on invertebrates, with their diet dominated by freshwater shrimp (O.Amphipoda, Gammarus and Hyalella) and dragonfly nymphs (S.O.Anisoptera, Aeshna and Macromia). Data indicate a marked dietary shift in August characterized by a decrease in the frequency of occurrence of the dominant invertebrates and an increase in the frequency of occurrence of vertebrates, particularly perch, from 0 percent in July to 38 percent in August. The categories of food items were combined into two general classes of vertebrates and invertebrates to test for significant changes in prey use on a month to month basis. Diet was independent of month for May, June, and July, with respect to both frequency of occurrence ($X^2=0.14$, df=2, $P>0.9$, Figure 3.8) and percentage composition by number of individual items in each food category ($X^2=0.73$, df=2, $0.75>P>0.5$, Figure 3.8). However, there was evidence to indicate a shift in the diet of northern pike in Mere Lake in August in terms of frequency of occurrence of the two food categories ($X^2=22.09$, df=1, $P<0.005$, Figure 3.8) and percentage composition by number ($X^2=179.56$, df=1, $P<0.005$, Figure 3.8).

The mean total length of the pike collected for stomach content analysis suggests a bias towards larger adults; however, there was no significant difference in the frequency of occurrence of the two major prey categories in the stomach contents of pike less than 30 centimetres and pike greater than or equal to 30 centimetres for the combined May-June-July sample ($X^2=0.00$, df=1, $P>0.995$) and the August sample ($X^2=0.11$, df=1, $0.75>P>0.5$). In addition, there was no evidence to suggest a difference in the percentage composition by number of items in the major food categories between the two size classes for the combined May-June-July sample ($X^2=0.10$, df=1, $0.9>P>0.75$) and the August sample ($X^2=1.46$, df=1, $0.25>P>0.1$). Thus, this description of stomach contents can be considered representative of the adult component of the population.

Prey Distribution Relative to Pike

Ekman dredge samples were analyzed separately for the two major invertebrate prey types, anisopterans and amphipods, and for the two sample periods, July and August. The Wilcoxon signed-ranks test indicated no significant difference between duplicate samples for anisopterans and amphipods in both July and August (Table 3.3). Thus, duplicate samples were pooled for the analysis of depth distribution.

There were significantly more anisopterans in the 0-3 metre depth stratum than in the deep-water stratum in both July and August, and data indicate a concentration of anisopterans at a depth of 1 metre in July (Kruskal-Wallis and Mann-Whitney U tests, $P<0.05$, Figure 3.9). Selection by dragonfly nymphs for a depth of 1 metre in August was not significant (Kruskal-Wallis test, $P= 0.064$, Figure 3.9). Similarly, there were significantly more amphipods in the shallow-water stratum than in the deep-water stratum in both July and August (Mann-Whitney U test, $P<0.05$, Figure 3.10). There was no evidence of depth selection by amphipods within the littoral zone in July (Kruskal-Wallis test, $P=0.44$, Figure 3.10); however, the highest abundance of amphipods was found at a depth of less than 0.5 metres in the August sample (Kruskal-Wallis tests, $P<0.05$, Figure 3.10).

As Ekman dredge samples were collected, habitat was recorded; and for each anisopteran and amphipod found in a dredge sample, the habitat category of the dredge was noted. It was thus possible to examine habitat selection by the two major prey types by comparing habitat used to the habitat available in all dredge samples. In July and August, anisopterans exhibited selection for habitat characterized by the presence of submergent vegetation and were found in areas of emergent vegetation and habitat characterized by the absence of vegetation less than would be expected by chance (July: $X^2=49.19$, df=2, $P<0.005$, Figure 3.11; August: $X^2=35.48$, df=2, $P<0.005$, Figure 3.11). Amphipods showed selection for vegetated areas, both emergent and submergent, in July ($X^2=11.32$, df=2, $P<0.005$, Figure 3.12); however, in August, amphipods were found in areas of emergent vegetation more than would be expected by chance and habitats characterized by submergent vegetation or the absence of vegetation less than would be expected by chance ($X^2=147.41$, df=2, $P<0.005$, Figure 3.12).

There was no difference in the mean number of anisopterans collected in Ekman dredge samples in the 0 to 3 metre stratum between July and August (Mann-Whitney U test, $P>0.10$, Table 3.4). However, there were significantly more amphipods collected in the dredge samples in July than in August (Mann-Whitney U test, $0.05>P>0.025$, Table 3.4).

As an Ekman dredge sample represents invertebrates which are both on and buried beneath vegetation or substrate, it is conceivable that these samples do not represent prey items available to visual predators such as northern pike. To compare the habitat use of prey items visually available to the habitat use of prey items as indicated by Ekman dredge analyses, a sample of dragonfly nymphs was collected within the study basin in August ($n=45$). The nymphs were collected by snorkelling; and thus, the sample represents anisopterans which could be located visually. Sampling was restricted to less than 1.5 metres of water; however, all major habitat types were represented in this depth stratum.

Chi-square analysis indicates no significant difference between the visually collected sample and the August Ekman dredge sample of anisopterans with respect to the proportion of nymphs observed in the area of submergent vegetation ($X^2=1.09$, $df=1$, $0.5>P>0.25$). In addition, there was no significant difference between the mean total length of dragonfly nymphs in the two samples ($t=0.58$, $P=0.59$, log transformed data). It would appear that Ekman dredge samples can give an unbiased estimate of the size and habitat use of invertebrates such as anisopterans that are availabile to visual predators.

Consideration of the depth distribution and habitat use of the two major invertebrate prey types, in light of the distribution of northern pike within the lake, suggests overlap between predator and prey in that both were predominantly littoral in their distribution. With respect to habitat use within the littoral zone; anisopterans selected areas of submergent vegetation in both July and August , a habitat not heavily used nor selected by the northern pike. In July, there was a moderate degree of overlap between amphipods and northern pike, as amphipods showed selection for both emergent and submergent vegetation. The degree of overlap with respect to habitat use increased in August when amphipods selected for the zone of emergent vegetation, the habitat highly used and selected for by the adult pike.

The number of perch sightings and number of pike observed per 600 square metres as recorded in the broadscale littoral zone survey on a month to month basis is presented in Figure 3.13. There was no evidence of a change in the littoral distribution of northern pike with respect to preferred depth strata during June, July, and August. Perch were sighted very infrequently in the littoral zone in June and July; however, perch moved into the shallow littoral zone in August at which time northern pike showed a significant increase in the proportion of perch consumed (Kruskal-Wallis tests, $P<0.05$, Figure 3.13).

Thus, overlap in the littoral zone depth distribution of northern pike and perch was low in June and July and relatively high in August. This can be attributed not to the movement of the predator but rather, to an apparent seasonal movement of perch into the peripheral areas of the lake.

Prey Type and Pike Foraging Rates

Effects of predator-prey interactions on the rate of foraging activity by northern pike in Mere Lake were examined indirectly through further analyses of stomach content data.

Adult pike showed a low percentage of empty stomachs in May, June, and July (5, 7, and 0%, respectively). In August, the percentage of empty stomachs showed a significant increase to 42 percent ($X^2=21.05$, df=2, $P<0.005$, Figure 3.14) concurrent with a significant decrease in the number of prey items per fish ($t=4.92$, $P<0.01$, log transformed data, Figure 3.14) and a significant increase in the mean size of prey items consumed per fish (Mann-Whitney U test, $z=-2.61$, $P=0.018$, Figure 3.14).

There was no relationship between prey size and predator size in the August sample ($r^2=0.097$, $P=0.11$). In the combined May, June, and July sample, the relationship was significant ($P<0.005$); however, only 9 percent of the variation was explained by the relationship between predator size and prey size ($r^2=0.090$); and the slope was relatively close to zero (slope[B]=0.027). Based on these results, values for prey size were not corrected for predator size. In addition, values for number of items per predator were not corrected for predator length; as there was no correlation between number of prey items consumed and predator size for the combined May, June, and July sample ($r^2=0.0069$, $P=0.20$) or for the August sample ($r^2=0.00064$, $P=0.46$).

The foraging rate of the adult pike in Mere Lake decreased in August as their diet shifted to include a significantly higher proportion of fish. Evidence to support this conclusion include: a high percentage of empty stomachs in August, a significant decrease in the number of food items per fish, and a corresponding increase in mean prey size.

Prey Selectivity

Pike exhibited selection for larger prey items than would be expected if food items were consumed at random. The mean size of anisopteran consumed in July and August was significantly larger than the mean size of anisopteran available within the littoral zone ($t=8.11$, $P<0.01$, Table 3.5) as determined from Ekman dredge data. Similarly, the mean size of amphipod consumed was significantly larger than the mean size of amphipod available within the environment of the predator (Mann-Whitney U test, $z=-8.95$, $P<0.01$, Table 3.5).

The mean size of perch consumed by the adult pike was 7.6±1.1 cm ($n=16$, range=6.0-9.5 cm).

D. DISCUSSION

Distribution Patterns, Microhabitat Use, and Microhabitat selection

The selection exhibited by northern pike in Mere lake for emergent vegetation and deadfall emphasizes the importance of macrophyte structure as a primary determinant of distribution in this population. The selection for vegetation, in particular, the selection for emergent vegetation and deadfall exhibited by northern pike in Mere Lake may be related to the predatory stalking-lunge strategy used by this species and the associated cover requirement. Grimm (1981b, 1983) in a study of four stocked ponds, concluded that vegetated regions are preferential areas for northern pike; and he presented evidence to suggest that the abundance of vegetation is a limiting factor controlling the biomass of small pike. In addition, Grimm reported a direct relationship between the standing stock of pike (<54 cm) and the surface area of aquatic vegetation supported by manipulative experiments involving the removal and regrowth of macrophytes.

Northern pike generally use a specialized stalking attack which is characterized by the following behavioral sequence: motionless orientation or axial tracking -- stalk (specialized movements of pectoral and dorsal fins) -- lunge -- chase. The latter occurs infrequently, as pike lack the stamina for a long pursuit (Hoogland et al. 1956, Nursall 1973, Neill and Cullen 1974). Webb and Skadsen (1980) presented evidence to suggest that the foraging tactics of Esox are largely genetically determined. The ambush strategy tends to be most effective against unalarmed prey and thus may demand a source of cover (Hobson 1974).

For northern pike, the use of emergent vegetation or other structural features of the shallow water environment such as deadfall may be a prerequisite for an efficient foraging repertoire. Dense stands of submergent vegetation, such as Chara, although used by juvenile pike as a source of cover may prove impenetrable to the larger adults and may be considered unavailable as a cover mechanism.

An integration of the factors considered as possible determinants of pike distribution patterns in Mere Lake would suggest that abiotic factors such as water temperature and dissolved oxygen concentration may have set ultimate bounds on the depth distribution of the northern pike within the lake. However, within the selected depth stratum, microhabitat use was finely tuned to the availability of cover, emergent vegetation and deadfall.

In Mere Lake, northern pike were always observed in the epilimnion during the daylight hours of the summer months; and thus, the metalimnion (thermocline) may have served as a daytime barrier to the movement of the pike. Similar observations have been reported for the muskellunge, a close relative of the northern pike inhabiting two large Wisconsin lakes (Dombeck 1979), a number of fish species of Cazenovia Lake, New York (Helfman 1979), and the littoral species of two Michigan Lakes (Hall and Werner 1977).

The depth stratum used by the majority of northern pike in Mere Lake was characterized by temperatures ranging from 18.6 to 23.6 °C during June, July, and August. The optimum temperature for growth in northern pike as determined experimentally in the laboratory is 19 °C and 21 °C with respect to increase in biomass and increase in length, respectively (Casselman 1978). The northern pike of Mere Lake thus occupied an optimum temperature stratum with respect to growth throughout the majority

of the summer months. However; when water temperatures reached 22 to 23 °C in early August, there was no evidence to indicate selection by the pike for a deeper depth stratum closer to the optimal temperature. As suggested by Magnuson et al. (1979), northern pike may respond to the temperature resource axis not according to the predictions of behavioral thermoregulation, but rather, in conjunction with foraging resources and other environmental variables.

The depth stratum selected by northern pike in Mere Lake was characterized by a dissolved oxygen concentration at or above saturation levels throughout the summer months. Food consumption, conversion efficiency, and growth rate of fishes are maximal at 100 percent air saturation; and any decrease in dissolved oxygen concentration is reflected in some decrease in growth rate (Adelman and Smith 1970, Casselman 1978). In support of this generalization, Adelman and Smith (1970) presented evidence to indicate that the growth rate and food consumption of northern pike is reduced by any reduction in oxygen concentration when temperature is held constant, and this decrease becomes extreme when dissolved oxygen concentration levels fall below 3 to 4 mg/L at 18.6 °C (30 to 40% saturation). In the 4 to 6 metre depth stratum of Mere Lake, percent oxygen saturation dropped to less than 30 percent in June and July and less than 40 percent in August. Thus, the pike in Mere Lake occupied areas of optimum dissolved oxygen concentration with respect to growth rate, food consumption, and conversion efficiency. It is possible that the marked drop in dissolved oxygen concentration between 4 and 6 metres to levels below 4 mg/L presented a barrier to the movement of northern pike in Mere Lake setting ultimate bounds on the distribution of the population.

Distribution of Predator and Prey

The northern pike in Mere Lake showed no seasonal change in distribution pattern within the period of investigation despite a marked trophic shift in the latter part of the summer. It is conceivable that the shallow littoral distribution of the adult pike in Mere Lake may be partially explained by the distribution of their invertebrate prey. However, with respect to microhabitat use, there was little evidence to suggest concentrations of pike in areas characterized by high prey abundance. Dragonfly nymphs, the major prey items consumed by northern pike in May, June, and July exhibited selection for areas

characterized by the presence of submergent vegetation, a habitat neither heavily used nor selected by adult pike. There was a moderate degree of overlap between amphipod and pike distribution in July; however, in August, when amphipods exhibited a marked selection for the zone of emergent vegetation, they became less important in the diet of the pike.

The northern pike in Mere Lake appear to select the largest prey items available within a restricted shallow water habitat, the use of which is related to factors other than the distribution of their dominant prey items. This idea is further supported by the seasonal trophic shift in the Mere Lake population to include a high proportion of perch in their diet. This dietary shift was related to changes in the distribution of the perch, rather than the distribution of the predator. Data indicate a movement of perch into the shallow areas of the lake coincident with the trophic shift exhibited by the pike.

Similar findings to what was observed in the present study have been reported over many years in the northern pike population of Lake Windermere. This population exhibits marked seasonal trophic shifts despite a restricted use of water less than 6.5 metres in depth (Johnson 1966a). Perch are an important component of their diet throughout the year but are particularly abundant in pike stomachs from May to September, a fact which Frost (1954) attributed to the presence of perch in the shallows in spring and summer and their selection of deep water habitat in the winter and early spring. Charr are the main food of the Windermere pike population in November and December coincident with a spawning-related movement of charr into the shallow regions of the lake. Similarly, the consumption of brown trout is high from October to February, associated in part with the October-December breeding habits of the fish (Frost 1954). The pike of Lake Windermere appear to feed on whatever species is abundant within their relatively restricted shallow water habitat (Johnson 1966a).

Contrary to the results presented for the pike populations of Mere Lake and Lake Windermere, other authors have suggested that the distribution of preferred prey species is a controlling factor in the daytime distribution of Esocids. Helfman (1979) found a relationship between the distribution of chain pickerel (Esox niger) and the distribution of preferred prey fish. Both predator and prey were found in the deeper water of Cazenovia Lake. Similarly, Ivanova (1969) presented evidence based on gill net returns to

indicate temporary concentrations of northern pike in areas characterized by high prey abundance; and Bregazzi and Kennedy (1980) suggested that the non-territorial, wandering nature of the pike in a southern eutrophic lake indicated a distribution dictated by that of the prey species. It is suggested that the finer resolution in the description of microhabitat use and microhabitat selection of both predator and prey in Mere Lake than in other studies may account for the discrepancy in results.

Northern Pike - Habitat Specialists or Generalists?

The northern pike of Mere Lake may be classified as habitat specialists during the summer months ie. very restricted in their patterns of habitat use. Contrary to results presented in this investigation, relatively recent studies using telemetry as a method of describing habitat use and depth distribution patterns of northern pike have suggested that large pike are relatively versatile in their selection of habitat (Chapman and Mackay 1984a, Sullivan unpubl. data). In addition Grimm (1981b) provided evidence to indicate that large pike (>54 cm) use both open water and vegetated areas of the lake. These conflicting results may be attributed in part to telemetry methodology which tends to bias results towards larger members of the population. However, it is more probable that such differences relate to the morphological and limnological characteristics of the study site. The investigation of Chapman and Mackay (1984a) was carried out on a pike population in a relatively shallow mesotrophic lake (maximum depth of 9 m) which remains unstratified throughout the summer months (Makowecki 1973); and the study of Grimm (1981b) was on four small stocked ponds with mean depths ranging from 1.2-1.5 metres. In shallow lakes and ponds, the absence of stratification may increase the amount and type of habitat available to the resident pike populations facilitating increased versatility in habitat use. The relatively specialized habitat use observed in the pike of Mere Lake is in part, a reflection of lake stratification which sets ultimate bounds on the depth strata available thus limiting accessible habitat types.

Foraging Rate

The adult component of the pike population in Mere Lake exhibited a low percentage of empty stomachs, a relatively small mean food item size, and a relatively high number of food items per stomach in May, June, and July when the pike diet was dominated by invertebrates, namely anisopterans and amphipods. These stomach content characteristics may be related to the observed adult diet of small organisms which require more time to collect in the numbers necessary to sustain metabolism and growth, and thus, less time for the stomach to be empty.

In August, pike exhibited a marked trophic shift to include a high proportion of perch in their diet. Associated with this dietary change, northern pike showed a relatively high percentage of empty stomachs, a large food item size, and a small number of food items per stomach. Review of literature on various pike populations indicates that these stomach content characteristics are typical of piscivorous populations (Frost 1954, Seaburg and Moyle 1964, Nursall 1973, Mann 1976, Diana 1979a).

Diana (1979b) described two extremes of foraging strategies with respect to meal frequency and meal size. Type I feeders consume continuously and digest while feeding. Small items are consumed over a relatively long period of time. Type II feeders eat a meal quickly and then digest the food before feeding again. A meal is ingested over a relatively short period of time. What we indirectly observe in the Mere Lake pike population is a shift from a Type I foraging strategy in May, June, and July to a mode of feeding which approaches Type II in August. It would appear then, that the reduced foraging rate exhibited by the northern pike in August may be in part attributed to this seasonal trophic shift.

However, reduced foraging rates have been related to factors other than changes in prey use. During the summer months Lawler (1965) recorded the highest frequency of empty stomachs in July and attributed this to a restriction of pike feeding activity associated with high temperatures. Restriction of activity in Esocids related to increases in water temperature above the optimum is further supported by the work of Casselman (1978) and Dombeck (1979).

As the preferred depth stratum of pike in Mere Lake was characterized by water temperatures exceeding the optimum temperature recorded for pike (Casselman 1978)

during early August (Appendix II, Table 2), it is conceivable that this abiotic factor contributed to a reduced rate of foraging activity by northern pike as inferred from stomach content analyses.

Diana (1979b) reported a marked decline in the daily ration of both male and female northern pike in Lac Ste. Anne, Alberta between June and August. If monthly variation in daily ration is characteristic of pike populations, it is possible that the observed reduction in foraging rate may have been directly influenced by a decline in daily ration over the summer months.

Finally, reduction in the rate of foraging activity has often been attributed to reduced prey availability. If food supply becomes limiting, it would be bioenergetically efficient to reduce activity levels, particularly at higher temperatures (Casselman 1978). Christiansen (1976), in a study of the feeding and behavior of northern pike provided evidence to suggest that pike may react to prey shortages by restricting activity thus avoiding excessive hunting and increasing predatory efficiency.

In Mere Lake, there was little evidence to suggest a decrease in the prey abundance. Although, the total number of amphipods in the littoral area was significantly lower in August than in July; there was no decline in numbers within the zone of emergent vegetation. The August influx of perch into the shallow marginal areas of the lake suggests an increase in overall prey abundance in the late summer. Thus, it appears that the apparent reduction in foraging rate was not directly related to a limiting abundance of prey items.

The observed decline in the rate of foraging activity may be attributed primarily to the seasonal trophic shift observed in the pike population and may have been intensified by increased water temperature and decreased daily ration requirements.

Pike as Optimal Foragers

Can we justify the observed diet and restricted distribution of northern pike in Mere Lake with reference to optimality theory? The foraging strategies of this population are optimal if one considers selectivity, preference, abundance, and accessibility of prey items.

The lurking ambush strategy of northern pike may demand a source of cover if prey is to remain unalarmed. In Mere Lake, emergent vegetation and deadfall may fulfill this prerequisite for a successful strike tactic. Within this restricted shallow water habitat, northern pike exhibited selection for large prey size consuming larger anisopterans and amphipods than would be expected by chance. According to optimal foraging theory, the ingestion of a food type is independent of the abundance of that type but depends on the abundance of more highly ranked items (Charnov 1976). Although perch may be considered a preferred food item of northern pike relative to invertebrates, they were not selected by the predator in May, June, and July. During these months perch were available within the lake but were not accessible to the pike which were restricted in their habitat to the shallower regions of emergent vegetation. When these preferred food items (perch) became accessible to the pike through a movement into the shallower areas in August, they were selected over lower ranked items.

For top carnivores, other things being equal, it is bioenergetically efficient to take a small number of large prey items; as this allows the animal to consume a large amount of energy comparatively quickly. So in general, the value of a prey item increases with its size when prey are small relative to the predator (Ivlev 1961, Brooks and Dodson 1965, Werner and Hall 1976). The northern pike is generally piscivorous (Lagler 1956, Seaburg and Moyle 1964, Lawler 1965, Beyerle 1971, Diana 1979b, Bregazzi and Kennedy 1980), and this ecological role is reflected in various of its morphological features. (Bucke 1971, Tyler 1973, Keast 1978). In addition to a preference for a fish dominated diet, northern pike generally exhibit a selection for large prey size (Frost 1954, Ivlev 1961, Popova 1966, Mann, 1976, Diana 1979b). Thus, it would appear that the optimal diet for northern pike would be characterized by a high proportion of fish and a relatively small predator size - prey size ratio.

The adult pike of Mere Lake selected for large prey items within their restricted habitat and switched their diet to include a relatively high proportion of perch when these items became accessible, thus conforming to the predicted optimal strategy for the species.

Seasonal Trophic Shifts as Related to Spatial Resource Use and Foraging Patterns: an Integration

The results of this investigation into the effects of a seasonal trophic shift on the spatial resource use and foraging rate of northern pike in Mere Lake provide considerable insight into the nature of seasonal resource shifts in this species. It was hypothesized that a seasonal trophic shift would be reflected in a change in the distribution pattern and foraging rate of the pike population. It would appear that abiotic factors such as water temperature and dissolved oxygen concentration may have influenced the depth distribution of northern pike in Mere Lake. However, within the selected depth stratum (<1.0 m of water) the microhabitat use of the pike was finely tuned to the availability of cover, an advantageous strategy for an ambush predator. Within their restricted shallow water habitat, the pike of Mere Lake selected for large prey size but did not concentrate in areas of highest prey abundance. The seasonal trophic change exhibited by the pike population from an invertebrate dominated diet to a piscivorous feeding mode was reflected in a reduced foraging rate and a change in distribution overlap between predator and prey attributed not the the movement of the predator, but rather, to a seasonal movement of perch into the peripheral areas of the lake.

Table 3.1.

Description of transects used to assess the depth distribution and microhabitat use of northern pike in Mere Lake during the summer months of 1983 (Basin I study area).

TRANSECT NUMBER	MEAN DEPTH	DIMENSIONS	TRANSECT CHARACTERISTICS	
T1	.4 m	200 m x 3 m	55% Emergent:	52% *Typha* 3% *Sparganium*
			38% Submergent:	21% *Ceratophyllum* 17% *Potamogeton*
			7% Deadfall	
T2	.6 m	175 m x 3 m	81% Emergent:	81% *Sparganium*
			10% Submergent:	8% *Potamogeton* 2% *Ranunculus*
			9% Silt	
T3	.9 m	100 m x 3 m	100% Submergent:	100% *Chara*
T4	1.5 m	100 m x 3 m	63% Silt	
			37% Submergent:	24% *Chara* 8% *Ceratophyllum* 5% *Ranunculus*
T5	1.8 m	100 m x 3 m	100% Submergent:	41% *Myriophyllum* 37% *Potamogeton* 22% *Ceratophyllum*
T6	2.5 m	100 m x 3 m	100% Submergent:	44% *Potamogeton* 28% *Ceratophyllum* 28% *Myriophyllum*
T7	4.6 m	100 m x 3 m	100% Silt	

Table 3.2.

Water temperature and dissolved oxygen concentration at 2 metre intervals in Basins I-V, Mere Lake, summer months, 1983. Both parameters were measured at the deepest portion of each basin. Each value represents the average of duplicate samples.

DATE	DEPTH (m)	BASIN I	BASIN II	BASIN III	BASIN IV	BASIN V
		O (mg/ℓ) T(^{O}C)	O (mg/ℓ) T(^{O}C)	O (mg/ℓ) T(^{O}C)	O (mg/ℓ) T(^{O}C)	O (mg/ℓ) T(^{O}C)
May 14	0	14.8 11.6	14.5 12.0	14.2 12.4	14.4 12.0	14.0 12.3
	2	15.3 11.2	14.5 11.8	14.3 11.7	14.5 11.2	14.1 12.0
	4	12.3 9.9	11.0 10.1	11.8 9.9	7.3 8.2	3.3 9.3
	6	8.5 8.3	1.7 6.9	1.4 5.6	0.8 4.5	1.2 5.5
	8	3.3 6.5	1.5 4.5	0.6 4.2	0.2 4.1	**** ****
	10	0.9 4.8	**** ****	**** ****	**** ****	**** ****
	12	0.0 5.3	**** ****	**** ****	**** ****	**** ****
June 29	0	9.6 19.0	10.6 20.3	9.7 19.8	9.9 20.2	10.5 20.2
	2	9.1 16.7	10.0 17.2	9.5 17.1	9.7 17.0	9.1 16.7
	4	8.1 15.4	8.2 15.6	6.6 15.1	7.4 14.8	5.9 15.3
	6	1.7 13.0	1.4 10.0	1.3 8.2	1.1 7.7	1.2 8.6
	8	1.1 7.9	**** ****	0.7 5.2	**** ****	0.7 5.6
	10	0.7 5.7	**** ****	0.3 4.9	**** ****	**** ****
	12	0.6 4.8	**** ****	**** ****	**** ****	**** ****
July 24	0	9.2 19.3	10.1 19.3	9.5 19.7	9.5 20.1	9.4 20.2
	2	9.4 19.1	10.0 19.1	10.0 19.5	9.5 19.7	9.0 19.6
	4	8.4 18.3	7.2 17.7	6.7 17.3	6.6 17.3	7.4 17.8
	6	1.8 13.8	1.3 11.7	1.5 9.4	0.2 8.6	0.7 10.1
	8	0.5 8.7	0.3 6.8	0.0 5.6	**** ****	0.6 6.3
	10	0.4 6.1	0.0 5.9	0.0 4.8	**** ****	0.4 4.9
	12	0.0 5.3	**** ****	**** ****	**** ****	**** ****
Aug. 22	0	10.3 19.4	10.3 18.9	10.6 19.0	10.0 19.3	9.9 20.5
	2	10.4 18.9	10.6 18.6	10.3 18.5	10.4 18.8	**** 19.1
	4	9.8 18.8	9.1 18.3	10.3 18.3	8.1 18.2	9.6 18.6
	6	4.2 15.5	3.7 13.0	3.3 10.7	3.8 10.1	3.3 11.6
	8	2.6 9.0	.8 6.9	**** 5.6	**** ****	1.3 6.3
	10	1.9 5.8	0.0 5.8	1.1 4.9	**** ****	.5 4.9
	12	1.9 4.9	**** ****	**** ****	**** ****	**** ****

Table 3.3.

Results of Wilcoxon's signed-ranks test for differences between duplicate Ekman dredge samples for anisopterans and amphipods in July and August, Mere Lake, 1983.

	MONTH	NUMBER OF SAMPLES	Z-VALUE	2-TAIL PROB.
Anisopterans	July	51	-1.17	0.241
	Aug.	50	-1.19	0.233
Amphipods	July	51	-1.00	0.317
	Aug.	50	-1.34	0.180

Table 3.4.

Mean number of amphipods and anisopterans per sample zone within the littoral area of Mere Lake in July and August, 1983 .

		MEAN	MANN-WHITNEY U STATISTIC	PROBABILITY LEVEL
Anisopterans	July	3.3	51.0	P>0.10
	Aug.	4.2		
Amphipods	July	25.2	72.5	0.05>P>0.025
	Aug.	11.5		

Table 3.5.

Prey selectivity by northern pike in Mere lake with respect to the two major invertebrate taxa consumed. Results presented are comparisons between the mean size of anisopterans and amphipods consumed, and the mean size of anisopterans and amphipods available in the environment as determined from Ekman dredge samples.

ANISOPTERANS

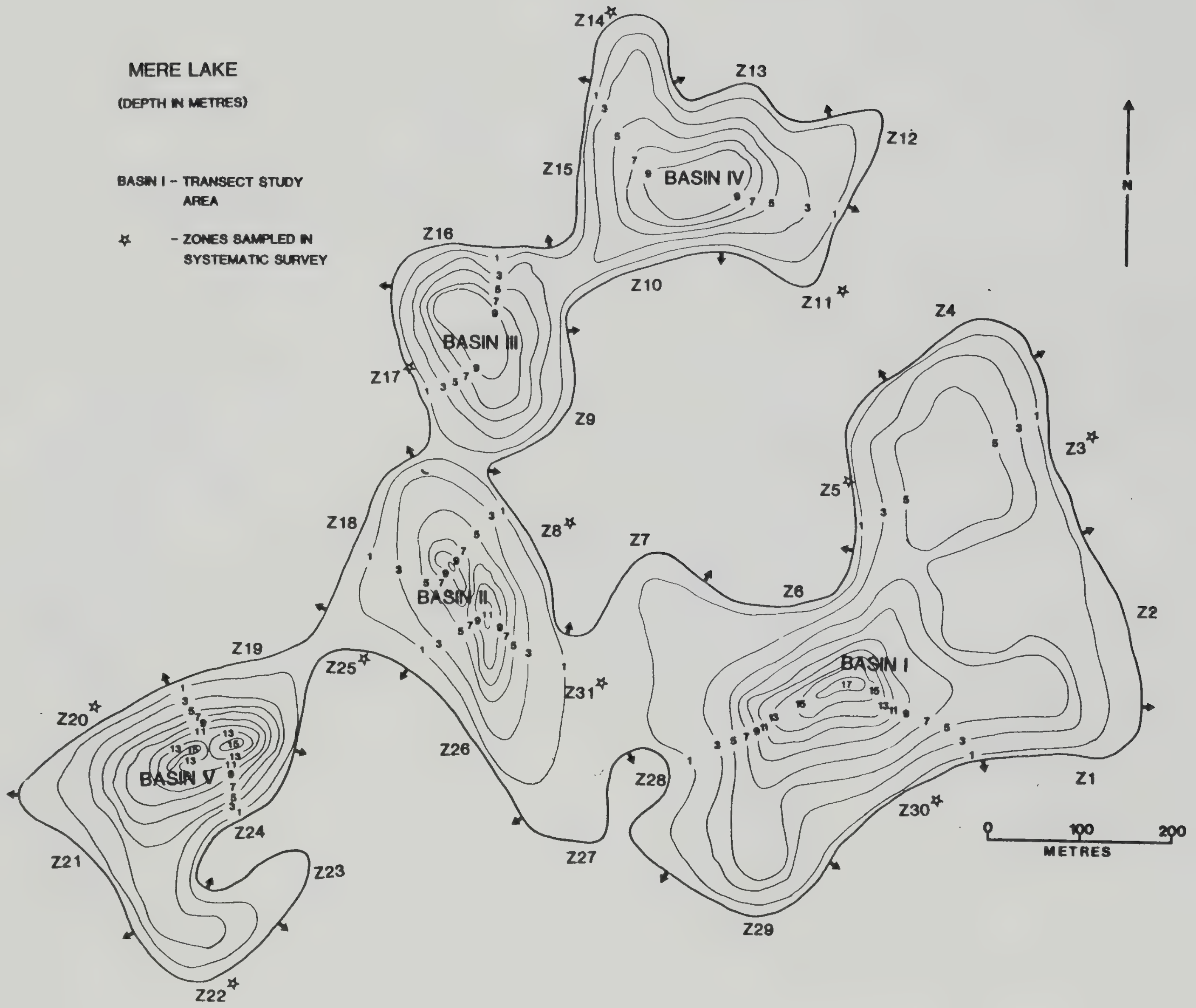
Sample	Sample Size (n)	Mean Total Length (mm)	Mean (log Transformed)	t Value	Prob.	95% C.I. (log transformed mean)
Consumed	64	25.47	1.18	8.11	P<0.001	1.15-1.21
Ekman Dredge	130	16.21	1.38			1.34-1.42

AMPHIPODS

Sample	Sample Size (n)	Mean Total Length (mm)	Mann-Whitney U Statistic	Prob.
Consumed	98	15.1	-8.95	P<0.001
Ekman Dredge	394	8.3		

Figure 3.1.

Mere Lake: bathymetric map, basin and zone demarcation. Depth data were obtained from Rhude (1979) and point samples in all basins.



MERE LAKE

(DEPTH IN METRES)

BASIN I - TRANSECT STUDY AREA

☆ - ZONES SAMPLED IN SYSTEMATIC SURVEY

Figure 3.2

Mere Lake: study area (Basin I), macrophyte distribution, and position of transect lines.

MERE LAKE

BASIN I - STUDY AREA

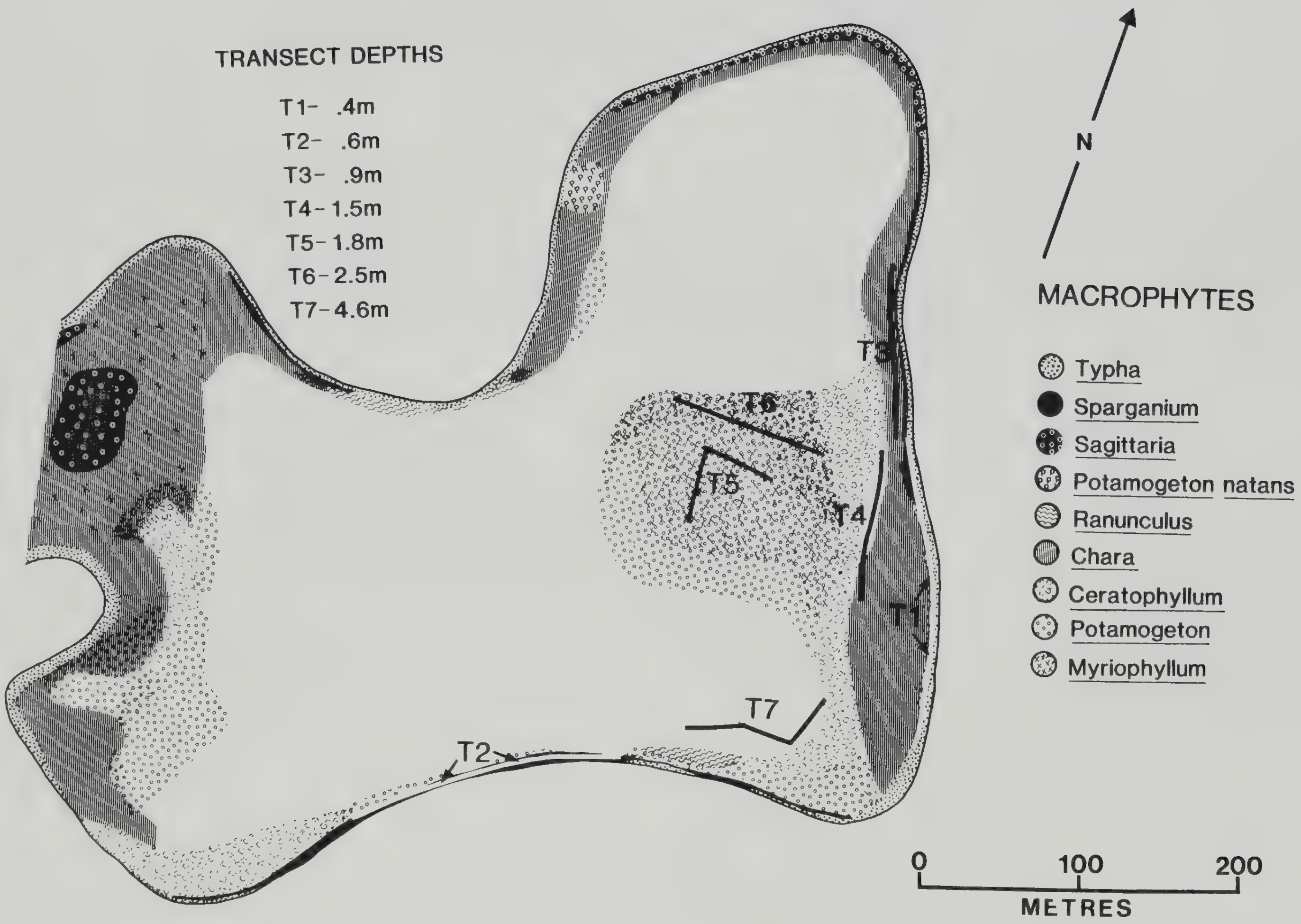
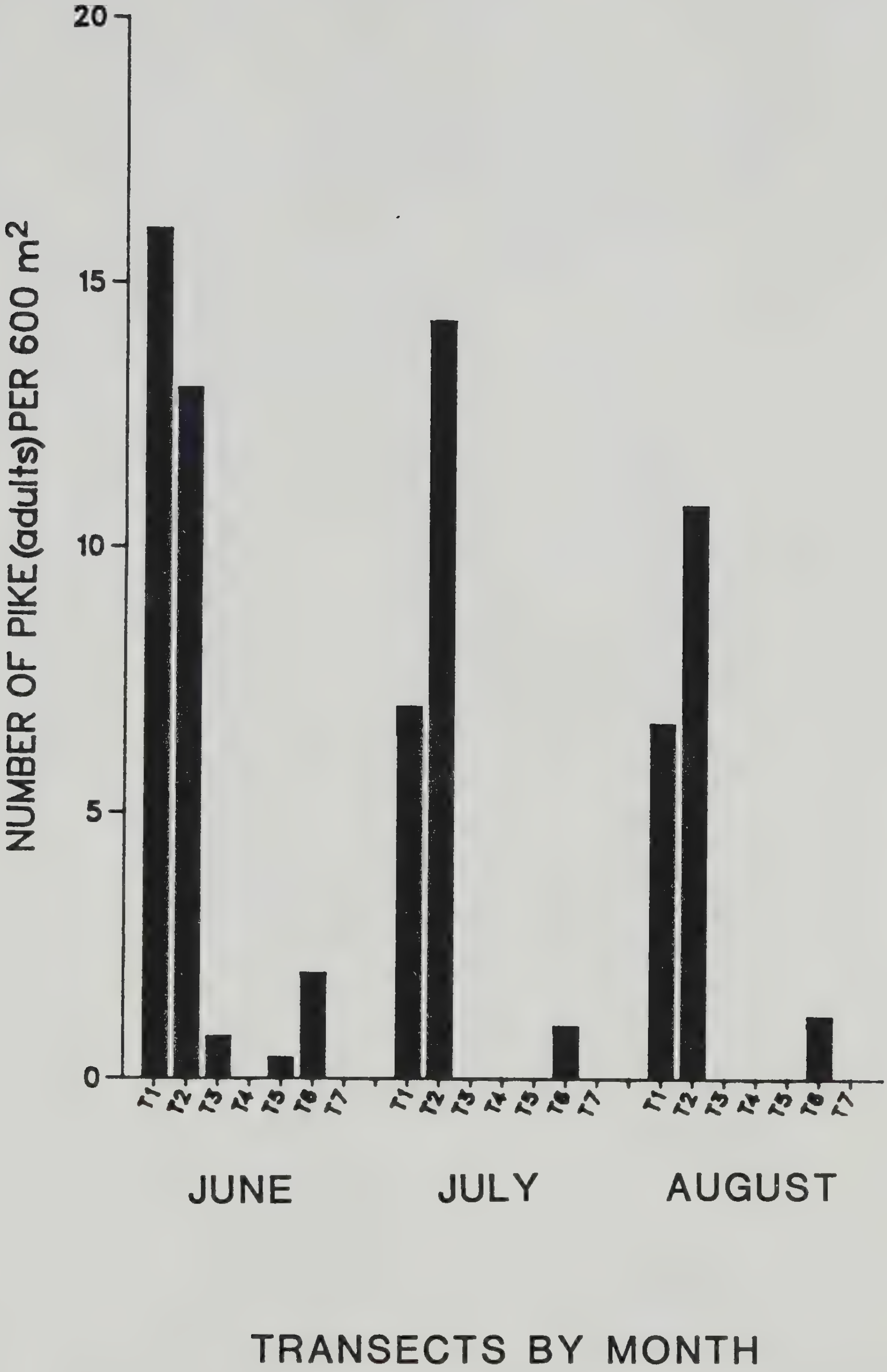


Figure 3.3.

Number of adult pike (age 1 year or older) observed on transects in Mere Lake during the summer months. Data were analyzed using the Kruskal-Wallis test for differences within groups of more than two transects and the Kruskal-Wallis multiple comparisons test for *a posteriori* comparisons between pairs of transects. Transect symbols underlined are not significantly different at $P<0.05$.

T1 - 0.5 m
T2 - 0.6 m
T3 - 0.9 m
T4 - 1.5 m
T5 - 1.9 m
T6 - 2.5 m
T7 - 4.6 m



T1T2T3T4T5T6T7 T1T2T3T4T5T6T7 T1T2T3T4T5T6T7

Figure 3.4.

Number of pike observed per 600 m^2 in Area A (<0.5 m), Area B (0.5-1.5 m), and Area C (1.5-2.5 m) in the systematic survey of the littoral area of Mere Lake. Each value is the average of 11 transects in a specified area. Data were analyzed using the Kruskal-Wallis test for differences between all three areas in a given month and the Kruskal-Wallis multiple comparisons test for *a posteriori* comparisons between two areas. Area symbols underlined are not significantly different at $P<0.05$.

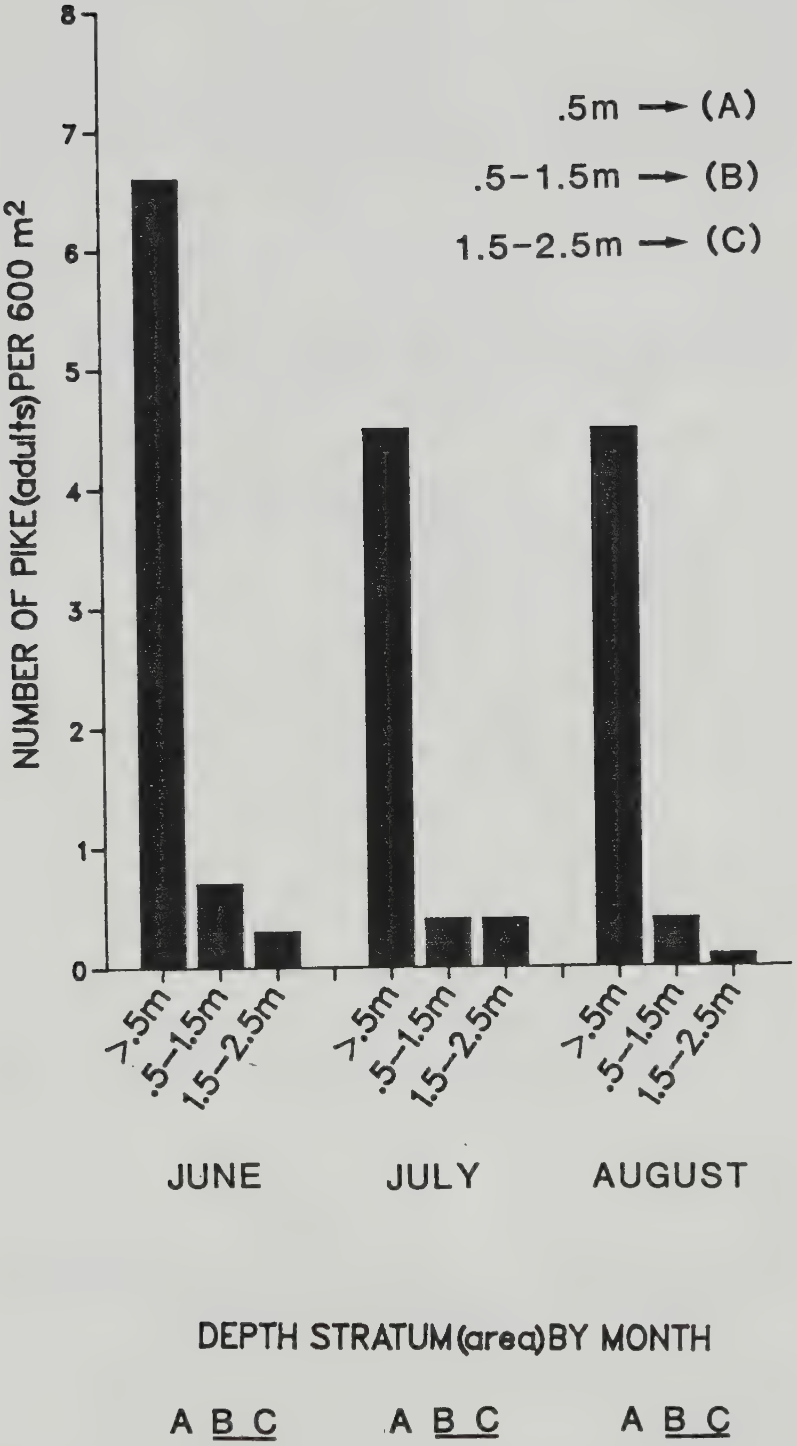
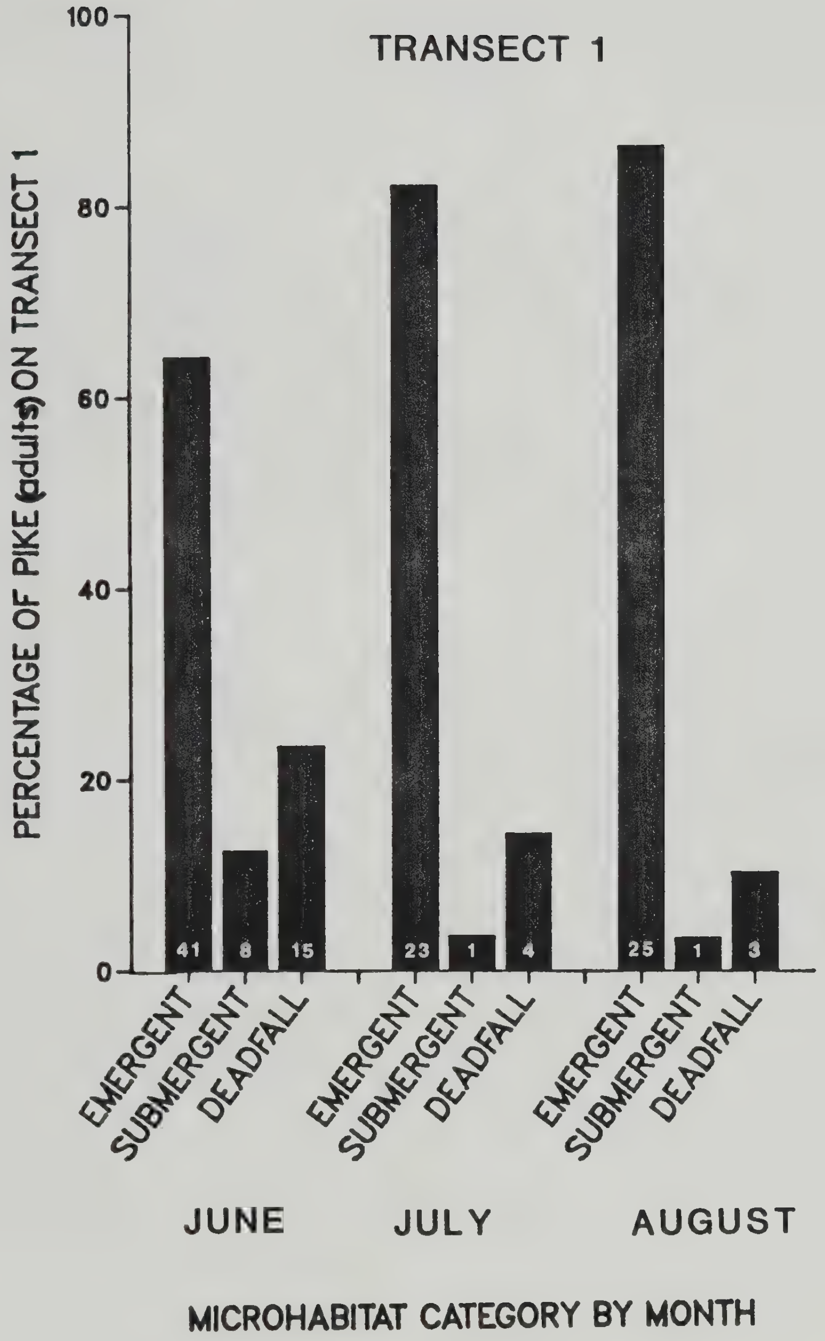

NUMBER OF PIKE (adults) PER 600 m²
0
1
2
3
4
5
6
7
8
.5m → (A)
.5-1.5m → (B)
1.5-2.5m → (C)
>.5m
.5-1.5m
1.5-2.5m
JUNE
JULY
AUGUST
DEPTH STRATUM (area) BY MONTH
A B C
A B C
A B C

Figure 3.5.

Percentage of adult pike (age 1 year or older) observed in each microhabitat category on Transects 1 and 2. Chi-square tests were performed on the raw data (presented at the base of each bar); percentages have been used for graphic representations.

Ho: microhabitat use is independent of month

Transect 1: $X^2=6.88$, df=4, $0.5>P>0.1$
Transect 2: $X^2=4.99$, df=2, $0.1>P>0.05$


TRANSECT 1
PERCENTAGE OF PIKE (adults) ON TRANSECT 1
100
80
60
40
20
0
41
8
15
23
1
4
25
1
3
EMERGENT
SUBMERGENT
DEADFALL
EMERGENT
SUBMERGENT
DEADFALL
EMERGENT
SUBMERGENT
DEADFALL
JUNE
JULY
AUGUST
MICROHABITAT CATEGORY BY MONTH

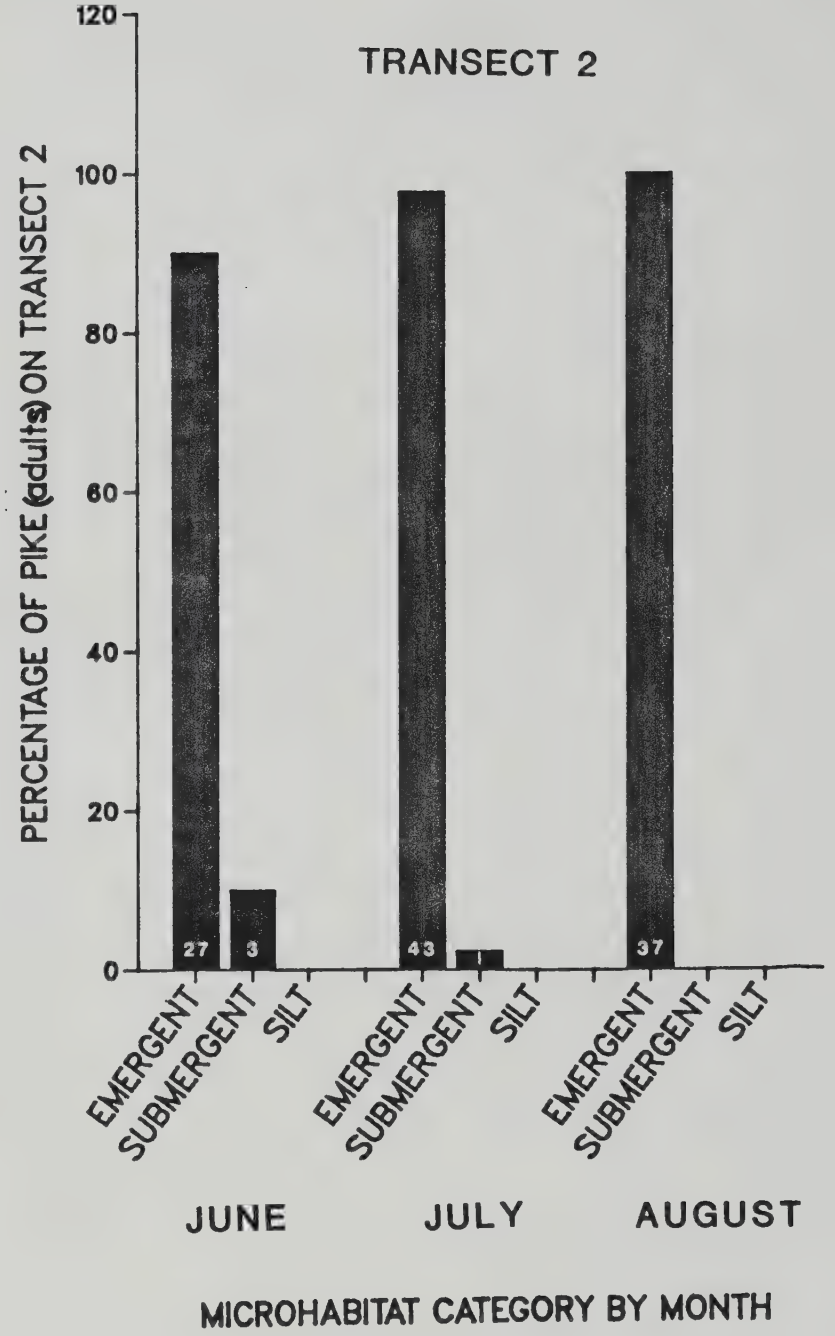
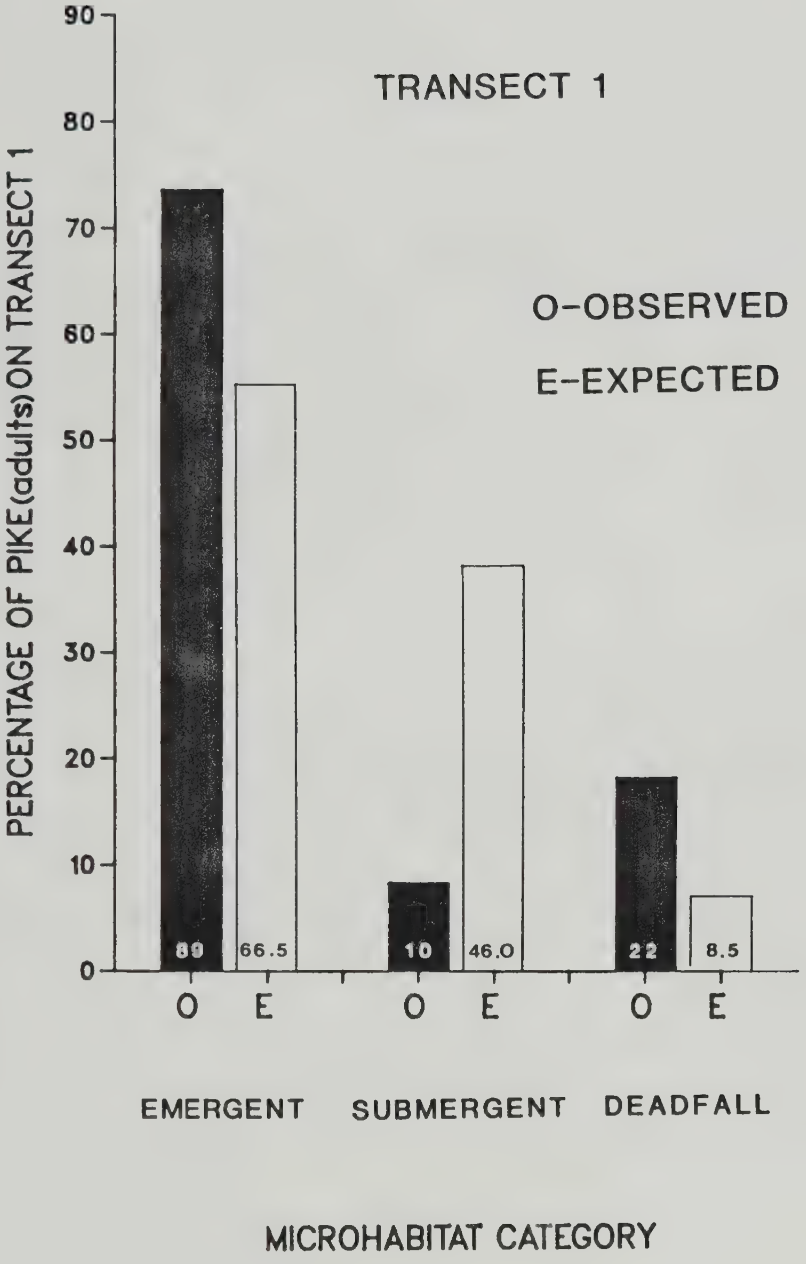

TRANSECT 2
PERCENTAGE OF PIKE (adults) ON TRANSECT 2
120
100
80
60
40
20
0
27
3
43
1
37
EMERGENT
SUBMERGENT
SILT
EMERGENT
SUBMERGENT
SILT
EMERGENT
SUBMERGENT
SILT
JUNE
JULY
AUGUST
MICROHABITAT CATEGORY BY MONTH

Figure 3.6.

Percentage of adult pike (age 1 year or older) observed and expected in each microhabitat category on Transects 1 and 2. Chi-square tests were performed on the raw data (presented at the base of each bar); percentages have been used for graphic representations.

Ho: there is no significant difference between the observed and the expected microhabitat use

Transect 1: $X^2=57.23$, df=2, $P<0.005$
Transect 2: $X^2=17.79$, df=2, $P<0.005$


TRANSECT 1
O-OBSERVED
E-EXPECTED
PERCENTAGE OF PIKE (adults) ON TRANSECT 1
0
10
20
30
40
50
60
70
80
90
89
66.5
10
46.0
22
8.5
O
E
O
E
O
E
EMERGENT
SUBMERGENT
DEADFALL
MICROHABITAT CATEGORY

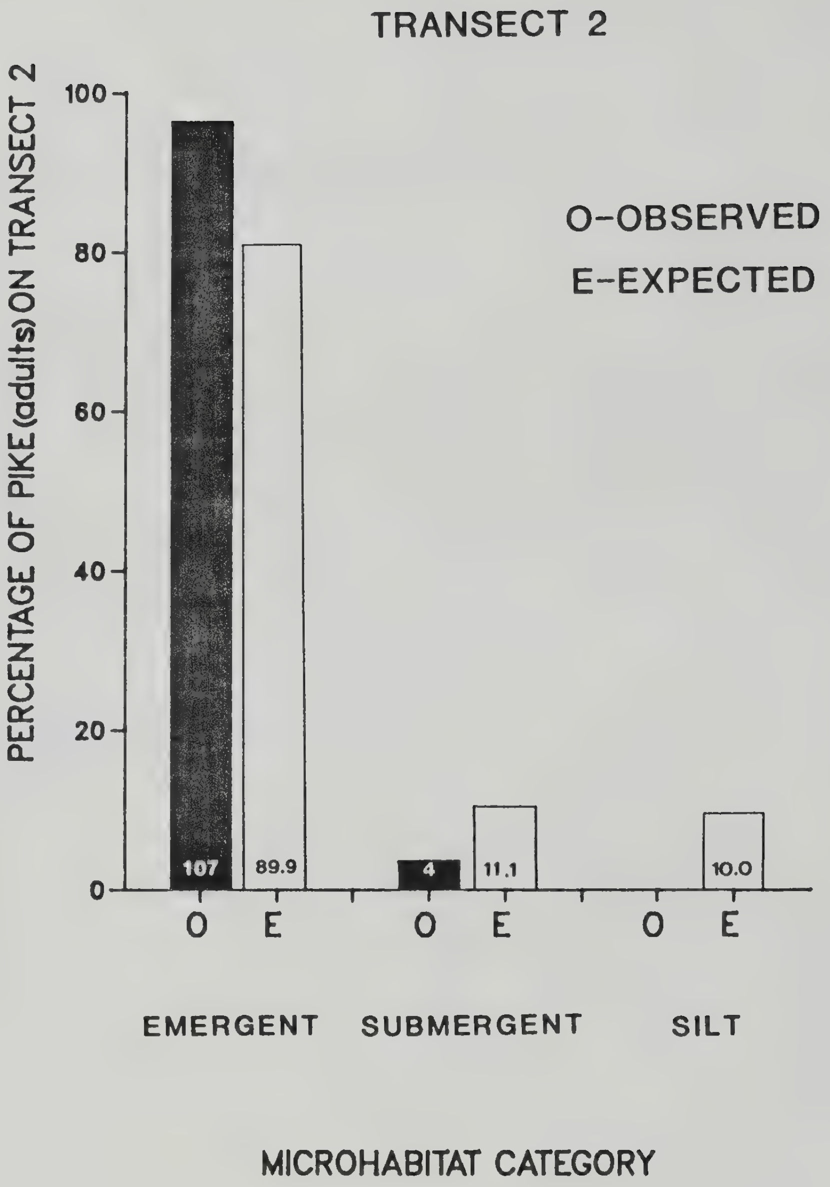

TRANSECT 2
O-OBSERVED
E-EXPECTED
PERCENTAGE OF PIKE (adults) ON TRANSECT 2
0
20
40
60
80
100
107
89.9
4
11.1
10.0
O
E
O
E
O
E
EMERGENT
SUBMERGENT
SILT
MICROHABITAT CATEGORY

Figure 3.7.

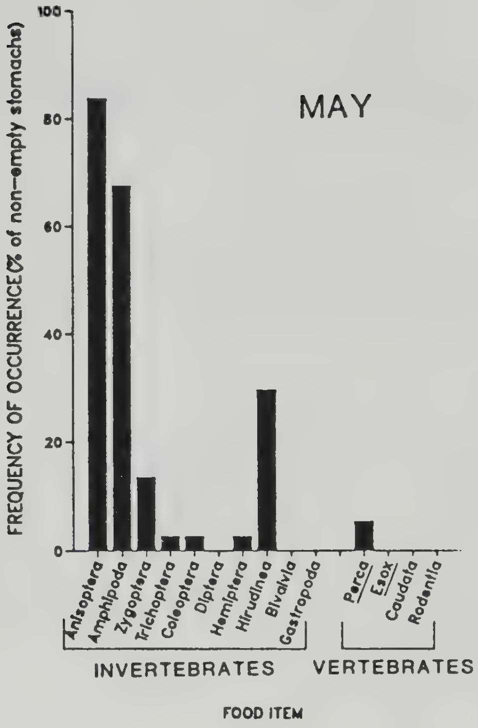
Frequency of occurrence of food items in the stomachs of adult pike (age 1 year or older) in Mere Lake during May, June, July, and August, 1983.

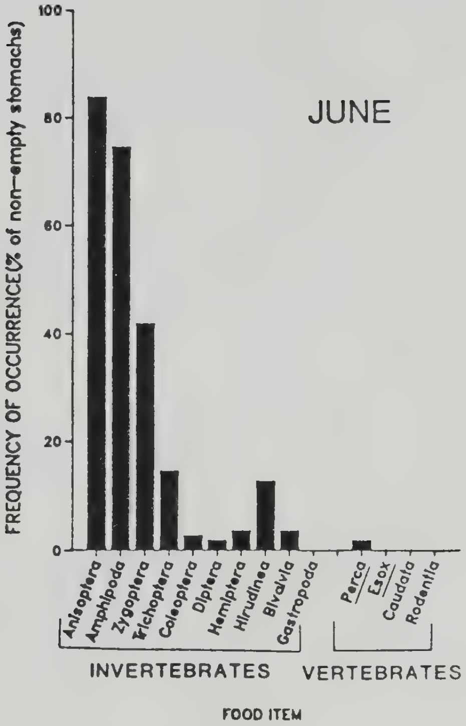
May: n=40
number of empty stomachs=2(5%)

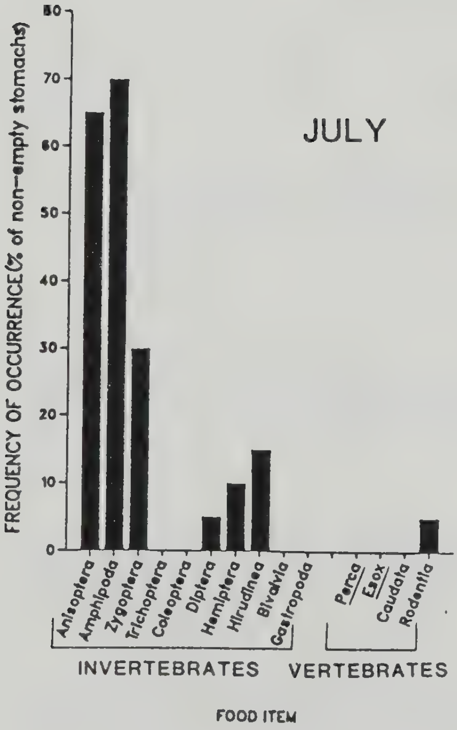
June: n=61
number of empty stomachs=7(12%)

July: n=19
number of empty stomachs=0(0%)

Aug.: n=36
number of empty stomachs=15(42%)


MAY
FREQUENCY OF OCCURRENCE(% of non-empty stomachs)
100
80
60
40
20
0
Anisoptera
Amphipoda
Zygoptera
Trichoptera
Coleoptera
Diptera
Hemiptera
Hirudinea
Bivalvia
Gastropoda
Perca
Esox
Caudata
Rodentia
INVERTEBRATES
VERTEBRATES
FOOD ITEM


JUNE
FREQUENCY OF OCCURRENCE(% of non-empty stomachs)
100
80
60
40
20
0
Anisoptera
Amphipoda
Zygoptera
Trichoptera
Coleoptera
Diptera
Hemiptera
Hirudinea
Bivalvia
Gastropoda
Perca
Esox
Caudata
Rodentia
INVERTEBRATES
VERTEBRATES
FOOD ITEM


JULY
FREQUENCY OF OCCURRENCE(% of non-empty stomachs)
80
70
60
50
40
30
20
10
0
Anisoptera
Amphipoda
Zygoptera
Trichoptera
Coleoptera
Diptera
Hemiptera
Hirudinea
Bivalvia
Gastropoda
Perca
Esox
Caudata
Rodentia
INVERTEBRATES
VERTEBRATES
FOOD ITEM

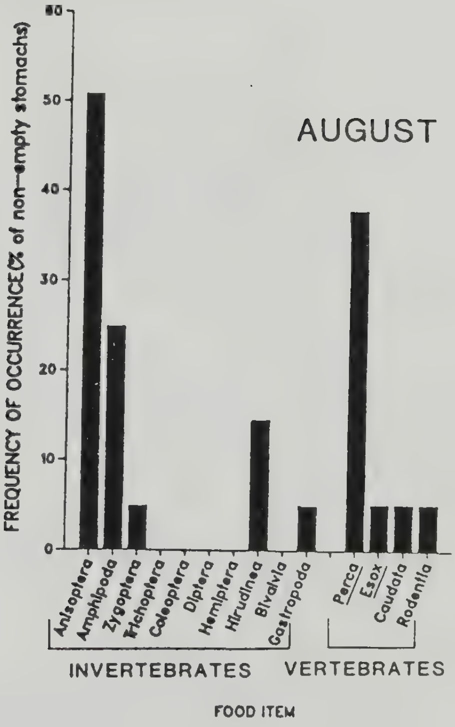

AUGUST
FREQUENCY OF OCCURRENCE(% of non-empty stomachs)
60
50
40
30
20
10
0
Anisoptera
Amphipoda
Zygoptera
Trichoptera
Coleoptera
Diptera
Hemiptera
Hirudinea
Bivalvia
Gastropoda
Perca
Esox
Caudata
Rodentia
INVERTEBRATES
VERTEBRATES
FOOD ITEM

Figure 3.8.

Stomach contents of adult pike (age 1 year or older) in Mere Lake during the summer months: frequency of occurrence and percentage composition by number of individual items in each food category. Chi-square tests were performed on the raw data (presented at the base of each bar); percentages have been used for graphic representations.

Ho: frequency of occurrence of food category is independent of month (May vs June vs July)

$X^2=0.14$, df=2, $P>0.9$

Ho: percentage composition by number of items in each food category is independent of month (May vs June vs July)

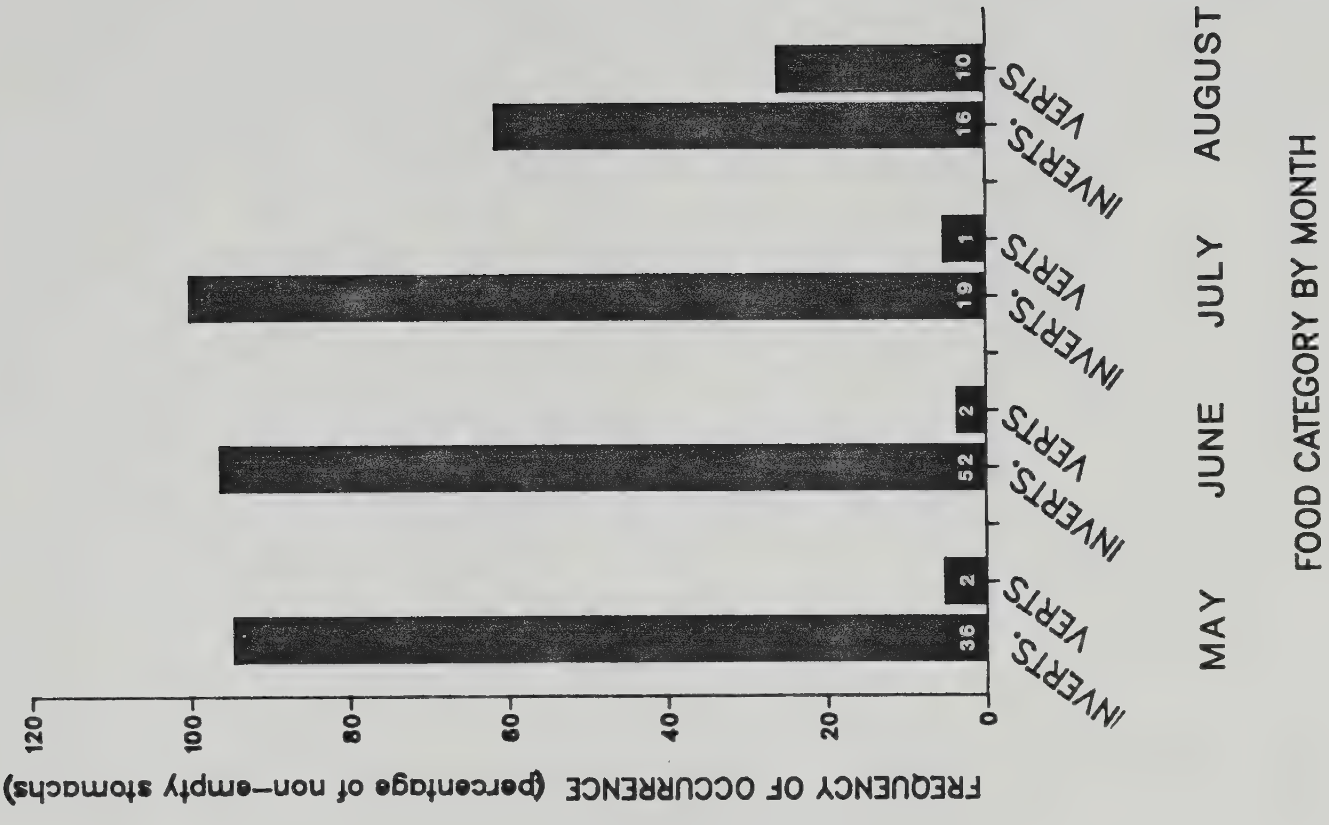
$X^2=0.73$, df=2, $0.75>P>0.5$

Ho: frequency of occurrence of food category is independent of month (May-June-July vs August)

$X^2=22.09$, df=1, $P<0.005$

Ho: percentage composition by number of items in each food category is independent of month (May-June-July vs August)

$X^2=179.56$, df=1, $P<0.005$


FREQUENCY OF OCCURRENCE (percentage of non-empty stomachs)
0
20
40
60
80
100
120
36
2
52
2
19
1
16
10
INVERTS.
VERTS.
INVERTS.
VERTS.
INVERTS.
VERTS.
INVERTS.
VERTS.
MAY
JUNE
JULY
AUGUST
FOOD CATEGORY BY MONTH

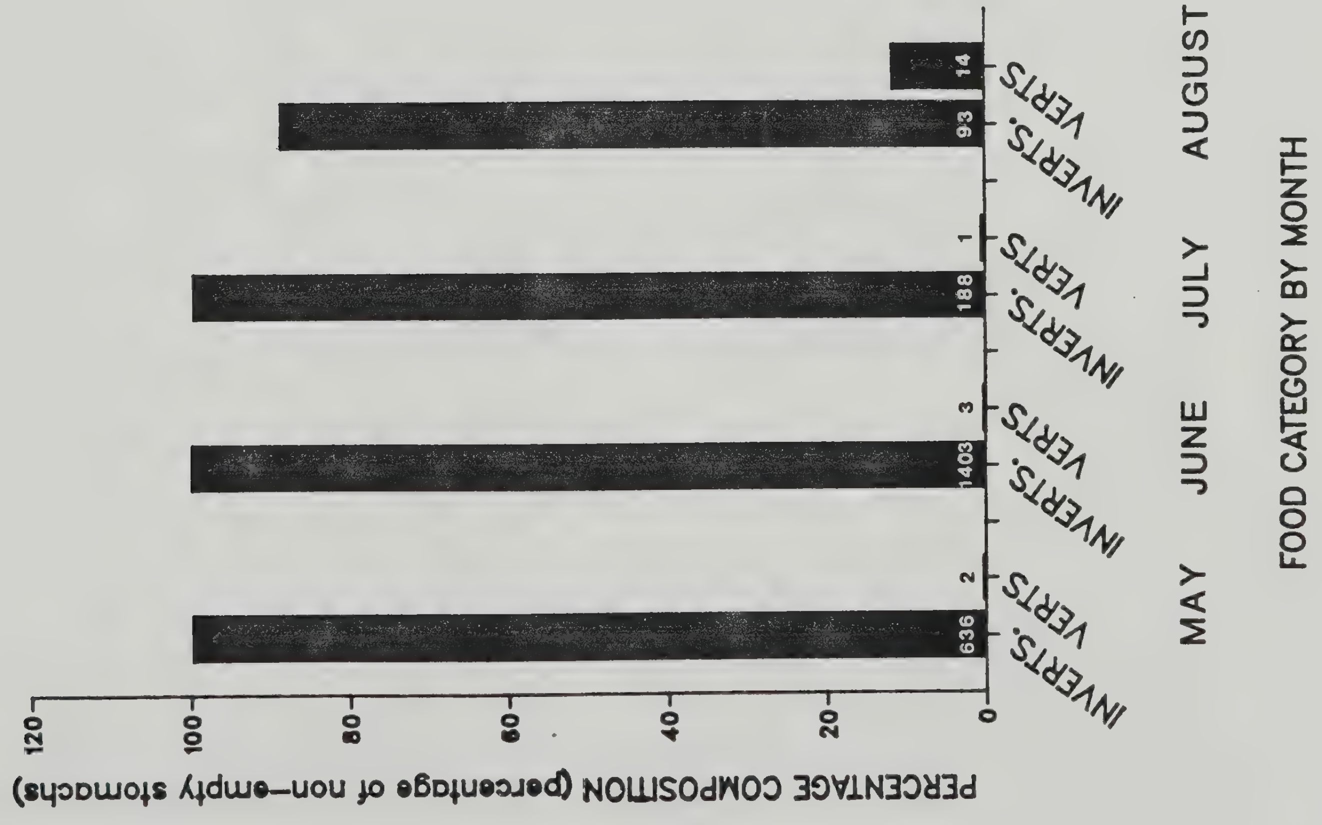
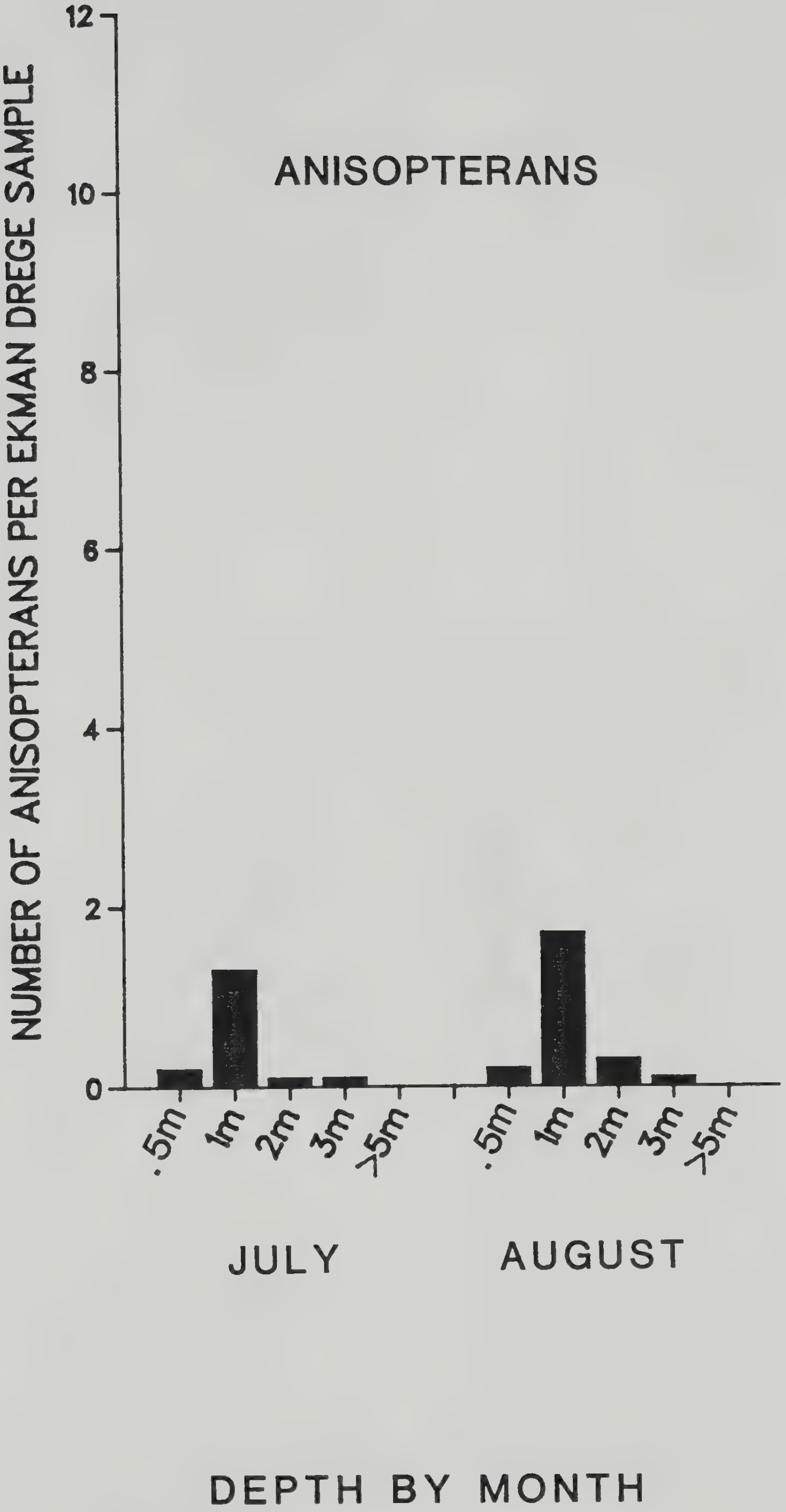

PERCENTAGE COMPOSITION (percentage of non-empty stomachs)
0
20
40
60
80
100
120
636
2
1403
3
188
1
93
14
INVERTS.
VERTS.
INVERTS.
VERTS.
INVERTS.
VERTS.
INVERTS.
VERTS.
MAY
JUNE
JULY
AUGUST
FOOD CATEGORY BY MONTH

Figure 3.9.

Depth distribution of anisopterans in Mere Lake in July and August, 1983. Depth distribution data were analyzed using the Mann-Whitney U test for differences between strata and the Kruskal-Wallis test for differences within each stratum and the Kruskal-Wallis multiple comparisons test for _a posteriori_ comparisons between two depths within a stratum. Depth symbols underlined are not significantly dffferent at $P<0.05$.


ANISOPTERANS
NUMBER OF ANISOPTERANS PER EKMAN DREGE SAMPLE
12
10
8
6
4
2
0
.5m
1m
2m
3m
>5m
.5m
1m
2m
3m
>5m
JULY
AUGUST
DEPTH BY MONTH

.5 1 2 3 <5 .5 1 2 3 <5

Figure 3.10.

Depth distribution of amphipods in Mere Lake in July and August, 1983. Depth distribution data were analyzed using the Mann-Whitney U test for differences between strata, the Kruskal-Wallis test for differences within each stratum, and the Kruskal-Wallis multiple comparisons test for *a posteriori* comparisons between two depths within a stratum. Depth symbols underlined are not significantly different at $P<0.05$.

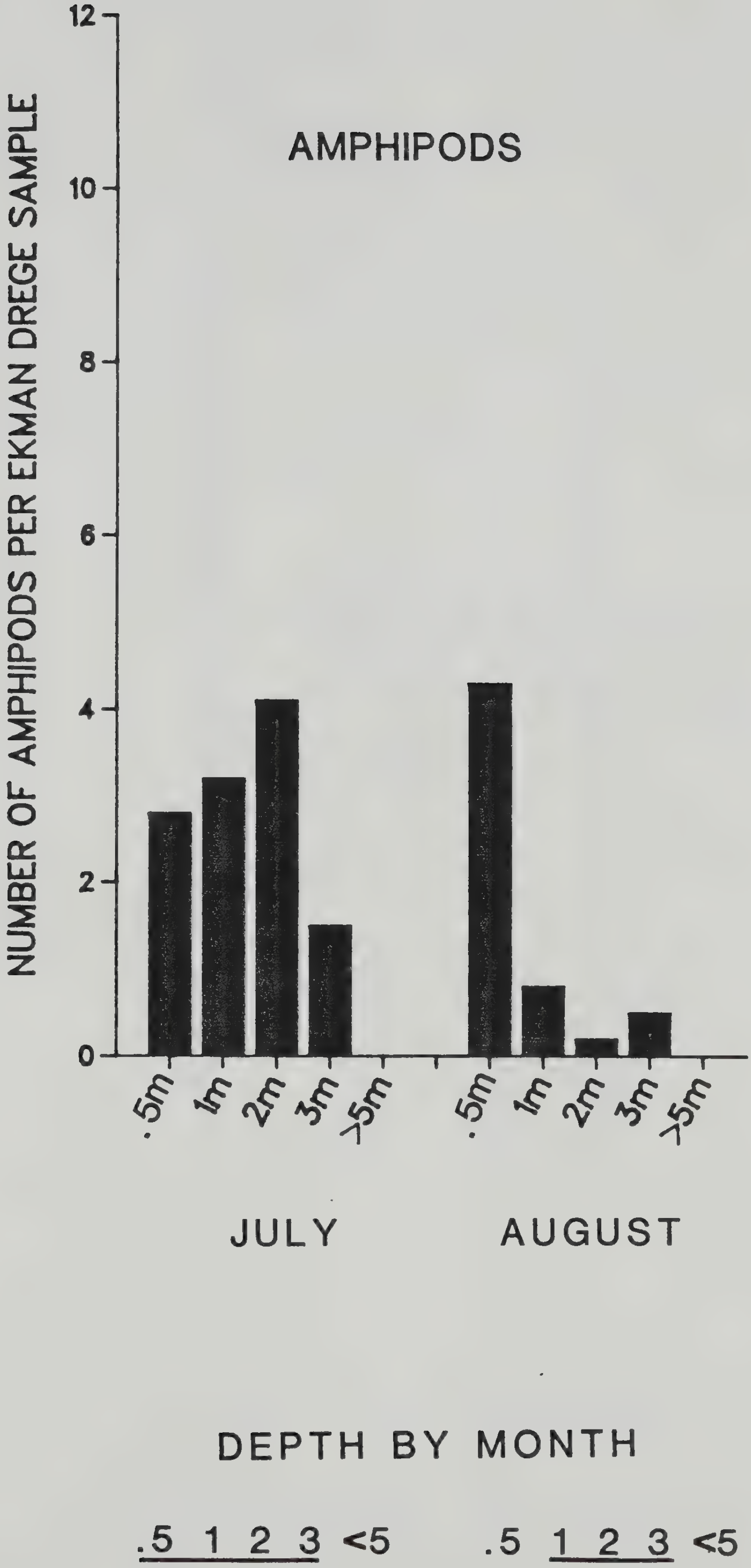

AMPHIPODS
NUMBER OF AMPHIPODS PER EKMAN DREGE SAMPLE
12
10
8
6
4
2
0
.5m
1m
2m
3m
>5m
.5m
1m
2m
3m
>5m
JULY
AUGUST
DEPTH BY MONTH
.5 1 2 3 <5
.5 1 2 3 <5

Figure 3.11.

Percentage of anisopterans observed and expected (based on habitat sampled) in each habitat category in July and August, Mere Lake, 1983. Chi-square tests were performed on raw the data (presented at the base of each bar); percentages have been used for graphic representation.

Ho: there is no significant difference between observed and expected microhabitat use

July: $X^2=49.19$, df=2, $P<0.005$
Aug.: $X^2=35.48$, df=2, $P<0.005$

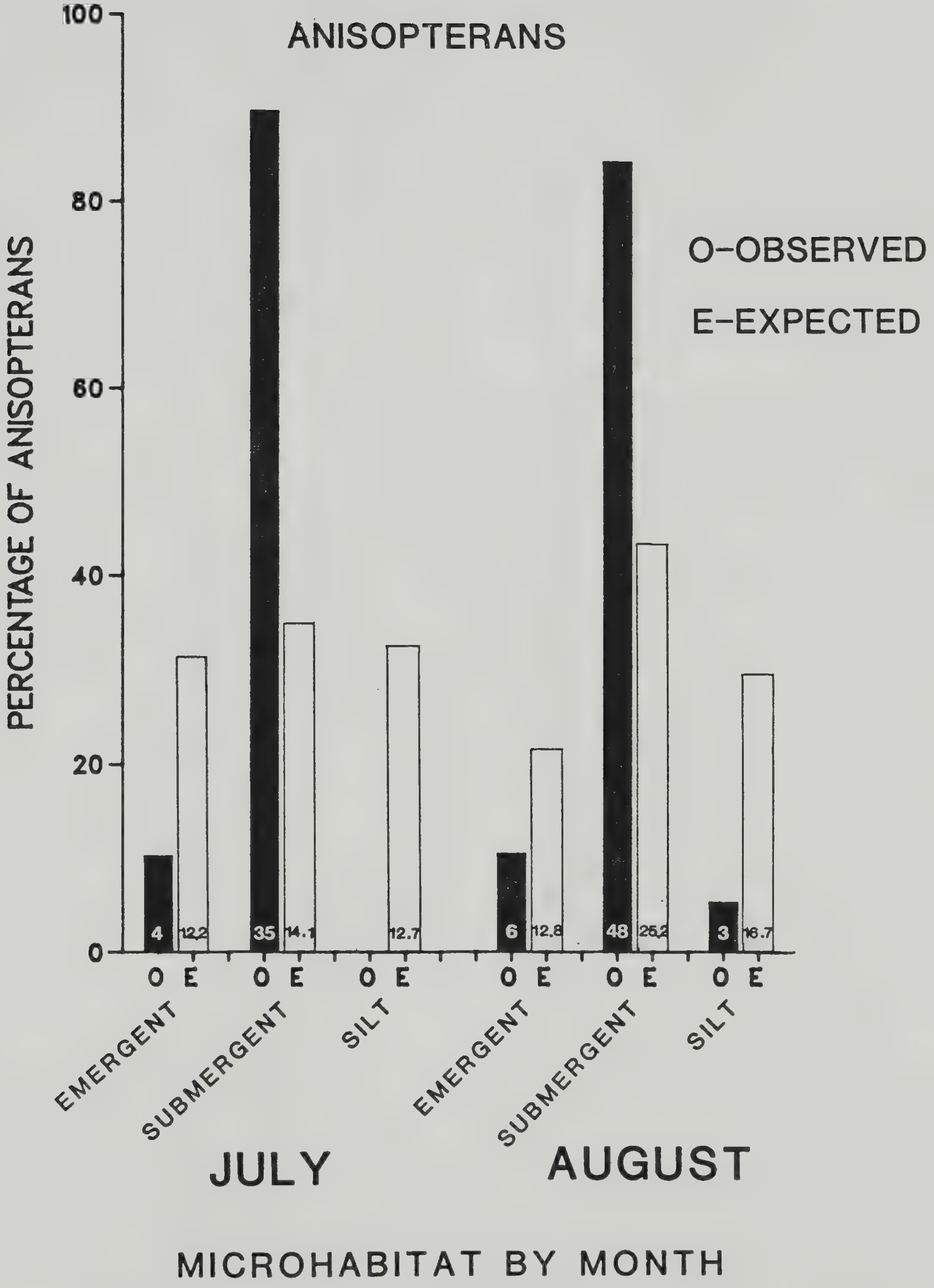

ANISOPTERANS
O–OBSERVED
E–EXPECTED
PERCENTAGE OF ANISOPTERANS
100
80
60
40
20
0
4
12.2
35
14.1
12.7
6
12.8
48
25.2
3
16.7
O E
O E
O E
O E
O E
O E
EMERGENT
SUBMERGENT
SILT
EMERGENT
SUBMERGENT
SILT
JULY
AUGUST
MICROHABITAT BY MONTH

Figure 3.12.

Percentage of amphipods observed and expected (based on habitat sampled) in each habitat category in July and August, Mere Lake, 1983. Chi-square tests were performed on the raw data (presented at the base of each bar); percentages have been used for graphic representation.

Ho: there is no significant difference between
observed and expected microhabitat use

July: X^2=11.32, df=2, $P<0.005$
Aug.: X^2=147.41, df=2, $P<0.005$

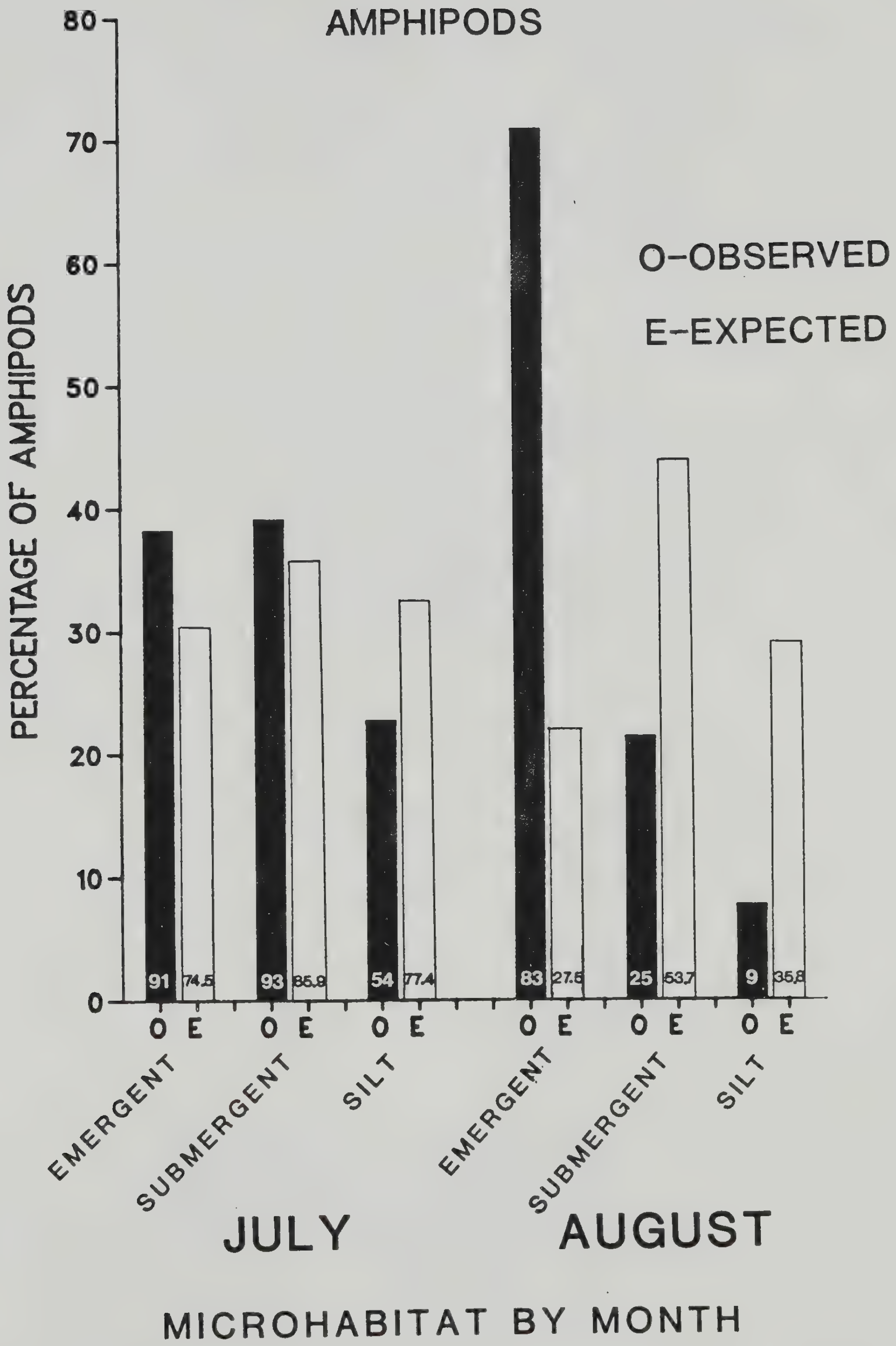
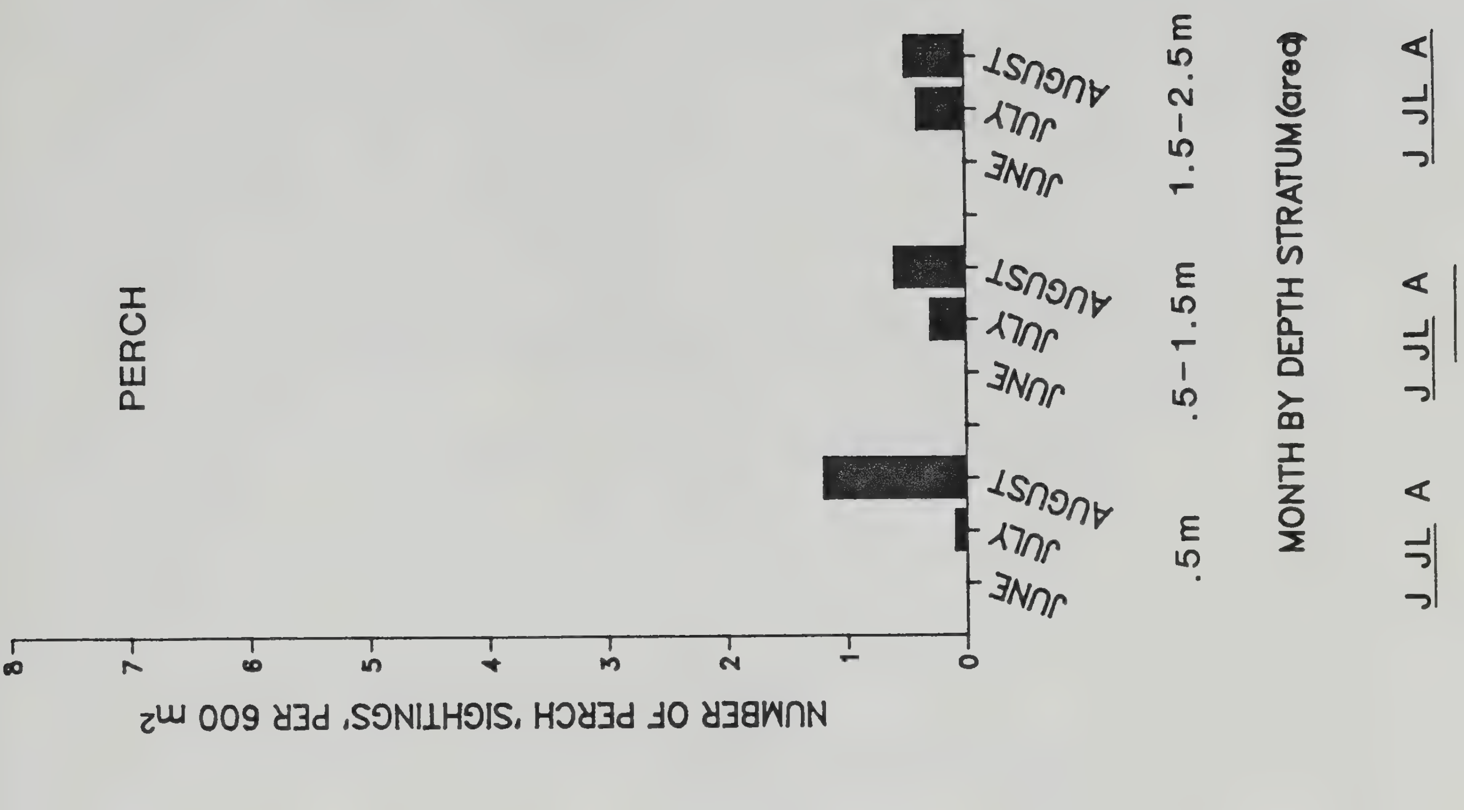

AMPHIPODS
O-OBSERVED
E-EXPECTED
PERCENTAGE OF AMPHIPODS
80
70
60
50
40
30
20
10
0
91
74.5
93
85.9
54
77.4
83
27.5
25
53.7
9
35.8
O E
O E
O E
O E
O E
O E
EMERGENT
SUBMERGENT
SILT
EMERGENT
SUBMERGENT
SILT
JULY
AUGUST
MICROHABITAT BY MONTH

Figure 3.13.

Number of perch 'sightings' and number of northern pike observed per 600 m^2 in Area A (<0.5 m), Area B (0.5-1.5 m), and Area C (1.5-2.5 m) in June, July, and August in the systematic littoral survey of Mere Lake. Each value is the average of 11 transects in a specified area. The data were analyzed using the Kruskal-Wallis test for differences between the three months in each area and the Kruskal-Wallis multiple comparisons test for *a posteriori* comparisons between months. Month symbols underlined are not significantly different at P<0.05.


PERCH
NUMBER OF PERCH 'SIGHTINGS' PER 600 m²
0
1
2
3
4
5
6
7
8
JUNE
JULY
AUGUST
JUNE
JULY
AUGUST
JUNE
JULY
AUGUST
.5m
.5–1.5m
1.5–2.5m
MONTH BY DEPTH STRATUM(area)
J JL A
J JL A
J JL A

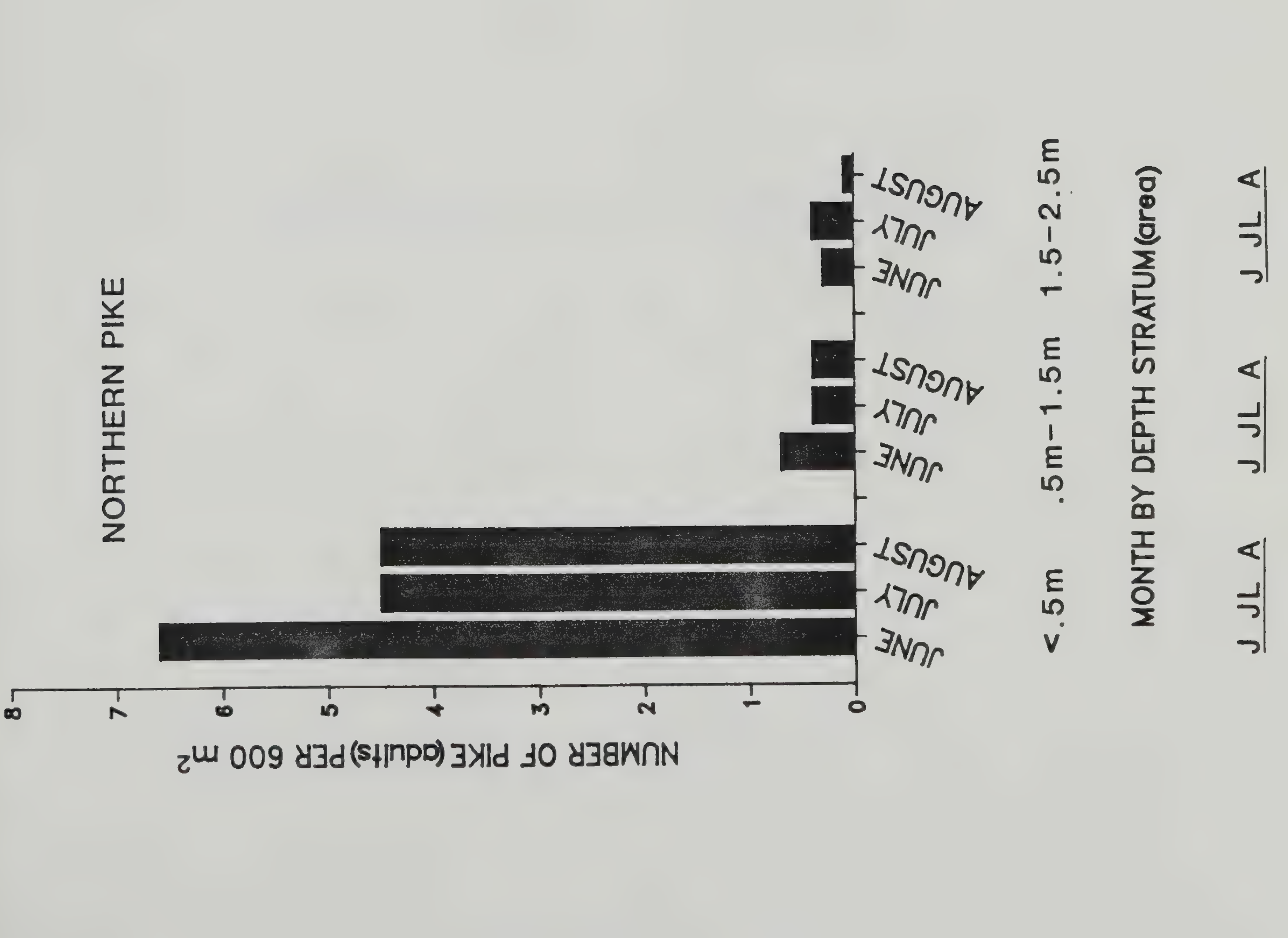

NORTHERN PIKE
NUMBER OF PIKE (adults) PER 600 m²
0
1
2
3
4
5
6
7
8
JUNE
JULY
AUGUST
JUNE
JULY
AUGUST
JUNE
JULY
AUGUST
<.5m
.5m–1.5m
1.5–2.5m
MONTH BY DEPTH STRATUM(area)
J JL A
J JL A
J JL A

Figure 3.14.

Percentage of empty stomachs, mean number of food items per fish, and mean length of food item per fish (mm) for the combined May-June-July sample (M-J-JL) and August sample (A) of northern pike in Mere Lake.

Ho: the percentage of empty stomachs is independent of month (M-J-JL vs A)

Test: Chi-square contingency test

$X^2=21.05$, df=2, $P<0.005$

Ho: there is a significant decrease in the mean number of food items per fish in August

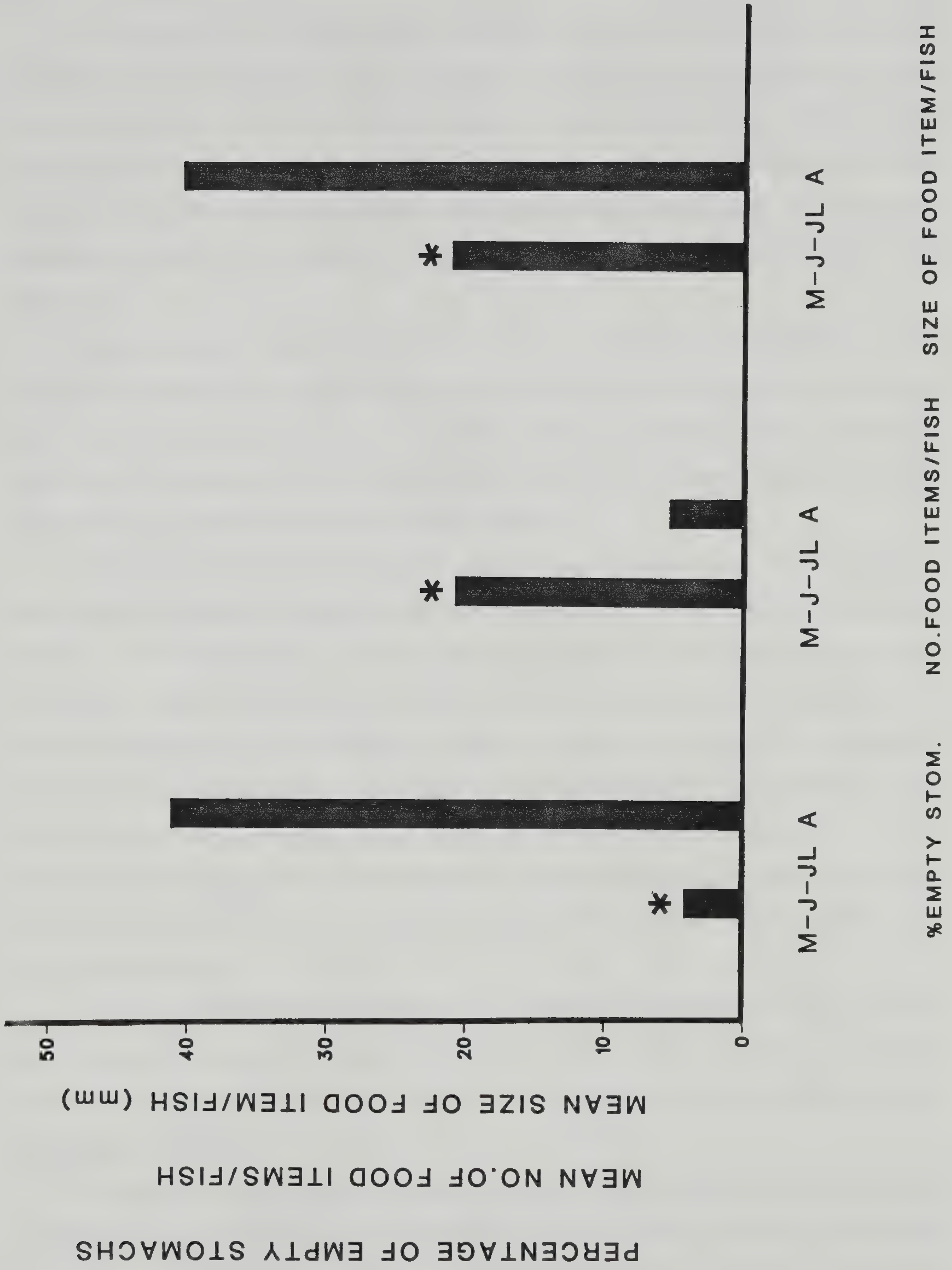
Test: t-test (log transformed data)

$t=4.92$, $P<0.01$

Ho: there is a significant increase in the mean size of prey item per fish in August

Test: Mann-Whitney U test

$z=-2.61$, $P=0.018$


PERCENTAGE OF EMPTY STOMACHS
MEAN NO.OF FOOD ITEMS/FISH
MEAN SIZE OF FOOD ITEM/FISH (mm)
0
10
20
30
40
50
M-J-JL A
M-J-JL A
M-J-JL A
*
*
*
%EMPTY STOM.
NO.FOOD ITEMS/FISH
SIZE OF FOOD ITEM/FISH

CONCLUDING DISCUSSION

The objective of this study was to assess the factors affecting the distribution and foraging activity of northern pike. The factors evaluated were a seasonal or monthly trophic shift and a size-related shift in addition to aquatic macrophyte distribution and various abiotic factors. By considering a number of variables it was possible to evaluate the importance of prey use as a factor influencing the foraging rates and distribution patterns of northern pike relative to additional variables which may affect these niche dimensions.

Field studies were conducted on two pike populations. Size-related dietary change was examined in Roi Lake, Alberta, where there were two distinct trophic classes of northern pike (young-of-the-year and adults). Seasonal or monthly dietary change was examined in Mere Lake, Alberta, where the adult segment of the pike population exhibited a marked trophic shift in the latter part of the summer.

Direct visual census of transects was the major technique used in this study to obtain data concerning microhabitat use, depth distribution, and activity of northern pike in addition to the distribution of the dominant prey items. Certain parameters of the underwater census technique were evaluated including independence of samples and the reaction of northern pike to observer presence. Samples were 92 percent independent, and the reaction of the pike to diver presence contributed approximately 4 percent error to the transect census results. The efficiency and precision of the visual method for the estimation of population size, microhabitat use, depth distribution, and dispersion pattern of northern pike; and minimal physical disturbance of the fish population warrants future use of this technique.

There was little temporal variation in the activity and microhabitat use by northern pike in Roi Lake during the daylight hours of the summer months. However, juvenile and adult pike showed differences with respect to microhabitat use, microhabitat selection, and dispersion pattern.

There was no evidence of a significant relationship between the distribution of juvenile pike in Roi Lake and the distribution of their major prey, the Iowa darter. Differences were observed between the microhabitat use of adult pike and their major

prey item, the dragonfly nymph.

Activity was primarily confined to the daylight hours during the summer months. However, activity as recorded by direct observation underwater did not adequately reflect the rate of foraging activity.

In Mere Lake, pike showed little variation in depth distribution and microhabitat use during the summer months, exhibiting selection for shallow areas (<1 m in depth) characterized by the presence of emergent vegetation.

Pike fed primarily on dragonfly nymphs and amphipods during May, June, and July; and stomach contents indicated a marked dietary shift in August characterized by a decrease in the frequency of occurrence of the dominant invertebrates and a significant increase in the frequency of occurrence of perch.

Overlap in the depth distribution of northern pike and the major invertebrate prey types consumed was exhibited in the predominantly littoral distribution of both predator and prey. There was a moderate degree of overlap in the microhabitat use of amphipods and pike; however, there was evidence of differential microhabitat selection between anisopterans and pike. Overlap in the depth distribution of pike and perch was low in June and July but relatively high in August.

It would appear that water temperature, dissolved oxygen concentration, and the presence of vegetation may have influenced the depth distribution of the northern pike in both populations. Within the selected depth stratum, ecological interactions appear to have been responsible for the finer resolution of microhabitat use, intraspecific predation pressure in the case of juveniles and foraging strategies in the case of adult pike.

The size-related trophic shift from a piscivorous diet to an invertebrate dominated diet in the pike population of Roi Lake was reflected in an increased rate of foraging activity in the adult segment of the population. This was attributed to an adult diet of small organisms which were necessarily consumed in greater numbers than the prey of juvenile pike.

The seasonal trophic shift exhibited by the adult northern pike of Mere Lake from an invertebrate dominated diet to a piscivorous feeding mode was reflected in a reduced foraging rate and a change in distribution overlap between predator and prey attributed not to the movement of the predator, but rather, to a seasonal movement of perch into the

shallow littoral areas of the lake.

Northern pike are generally piscivorous (Frost 1954, Lagler 1956, Seaburg and Moyle 1964, Lawler 1965, Beyerle 1971, Diana 1979a, Bregazzi and Kennedy 1980), and this ecological role is reflected in various morphological features. The alimentary tract of northern pike is typical of most top carnivores; the shovel-like snout, large mouth, enlarged and recurved marginal teeth, and the arrangement of the teeth are all adapted for seizing, holding, and directing large, slippery prey towards its stomach. In addition, the large stomach and relatively small intestine are related to a piscivorous diet (Bucke 1971, Tyler 1973, Keast 1978).

Body morphology generally enables one to make predictions with respect to the feeding ecology of a species; and one would predict based on morphological characteristics, that the diet of northern pike would be dominated by fish.

The appearance of invertebrates as a dominant prey type on both a seasonal and a size-related basis exemplifies an extreme degree of flexibility in the diet of this species.

The lurking-ambush strategy of northern pike has been described in a number of studies (Hoogland et al. 1956, Nursall 1973, Webb and Skadsen 1980) where pike have been presented with various fish species that were relatively active (stickleback, yellow perch, fathead minnow). Webb and Skadsen (1980) presented indirect evidence to suggest that the foraging tactics of Esox are largely genetically determined and have been strongly selected for over evolutionary time. Qualitative field observations in both Mere Lake and Roi Lake suggest that slow patterns of stalking and searching are also directed at relatively inactive benthic prey items such as Iowa darters and dragonfly nymphs. The predatory success rate of northern pike on various fish species ranges from 41 percent for perch (Nursall 1973), a prey fish which exhibits obvious defensive manoeuvers in response to pike, to 73 percent for fathead minnows, which in the experiments of Webb and Skadsen (1980) rarely attempted escape.

One would predict that a stalking-lunge foraging tactic when directed at slow moving benthic prey items such as anisopterans would result in a very high predatory success rate by northern pike comparable or greater than the success rate for fathead minnows. A higher capture rate may compensate for the greater number of prey items required to sustain a pike feeding primarily on invertebrates rather than other fish. Thus,

in a lake where forage fish are not readily accessible or accessible only on a seasonal basis, an invertebrate dominated diet may be an adaptive strategy providing that the invertebrate prey are abundant within the selected habitat of the pike. The plasticity in foraging strategy exhibited by northern pike in Roi and Mere Lakes may compensate for very restricted habitat use patterns exhibited by these two populations during the summer months.

Predictions with respect to the temporal stability of the distribution patterns observed in Roi Lake (1982) and Mere Lake (1983) are limited by a one-season analysis. However, I believe that certain speculations can be made based upon the nature of the factors considered to affect the depth distribution and microhabitat use observed in the two pike populations.

There was evidence to suggest that water temperature and dissolved oxygen concentration may have influenced the depth distribution of the two populations. These two parameters tend to show minor fluctuations on an annual basis with respect to the position of the thermocline and chemocline (Prepas and Vickery 1984, Prepas pers. comm.). Thus, insofar as dissolved oxygen concentration and water temperature determine spatial distribution of northern pike in Roi Lake and Mere Lake, one would expect the observed depth distribution patterns during the summer months to be relatively stable over time.

Aerial photographs of Mere and Roi Lakes taken in 1977 show very similar patterns of emergent vegetation distribution to those observed in the 1982 and 1983 field seasons. This suggests that the general configuration of the vegetation structure does not change markedly from year to year. As macrophyte structure appeared to be an important factor influencing the patterns of depth distribution and microhabitat use, a constant and predictable vegetation structure would promote stability in the habitat use patterns of the resident pike populations.

Although habitat use and depth distribution patterns have been studied in a number of pike populations, the value of the present investigation lies in the finer resolution in the description of depth distribution and microhabitat use than in other studies facilitated by the use of direct underwater observation. Previous investigations have tended to rely on indirect methods such as telemetry, gill netting, and mark-recapture for the evaluation of

habitat use patterns. In addition, the non-destructive nature of the study with respect to the pike populations allowed this investigation to be undertaken on very small, unproductive lakes where techniques involving high induced mortality would not have been suitable.

Results are inconclusive to the degree that no single factor could be considered to be the primary determinat of the habitat use patterns and foraging rates of the pike. Future studies in this area should address similar questions on a number of pike populations against various backgrounds of prey species. In addition, a comparative investigation of pike populations in stratified and unstratified lakes where diet is similar may be useful in evaluating more conclusively the influence of abiotic parameters on the habitat use and foraging rates in this species. Finally, the disadvantage of a one-season analysis in describing predictive patterns is obvious, and a longterm investigation is necessary to address the question of year-to-year stability in the patterns of distribution and foraging rates exhibited by northern pike.

North temperate freshwater fishes have evolved in a relatively unpredictable environment characterized by the advance and retreat of glaciers. In addition, a seasonal factor dominates northern lakes resulting in interrupted supplies of nutrients, highly variable temperatures, and seasonal loss of cover due to the die-back of various macrophyte species (Emery 1978, Keast 1978).

Temperate lakes are characterized by a low species richness of fish fauna relative to tropical ecosystems. In fact, tropical lakes are often five to 10 times as diverse as boreal lakes. The high diversity of fishes in tropical lakes is in part maintained by a high degree of morphological differentiation (Lowe-McConnell 1975, Emery 1978, Keast 1978). In north temperate fish communities, there is a relatively small degree of morphological diversification. Thus many temperate fishes tend to be less specialized with respect to foraging strategies than tropical freshwater species (Lowe-McConnell 1975, Keast 1978).

Plasticity in foraging strategies is exemplified in the size-related and seasonal trophic shifts of the northern pike in Roi and Mere Lakes and may represent an optimum adaptation for life in north temperate latitudes.

In summary, it was hypothesized that a size-related trophic shift and seasonal dietary change would be reflected in size-specific and seasonal changes in the depth distribution, microhabitat use, and foraging rate of northern pike in Roi and Mere Lakes. Results of this study support the idea that pike are opportunistic predators, selecting for the largest prey available within their preferred habitat. Depth distribution and microhabitat use were not heavily influenced by the habitat use of the major prey species; however, there was evidence to indicate that prey type was important as a factor influencing the foraging rate of the northern pike in Roi Lake and Mere Lake.

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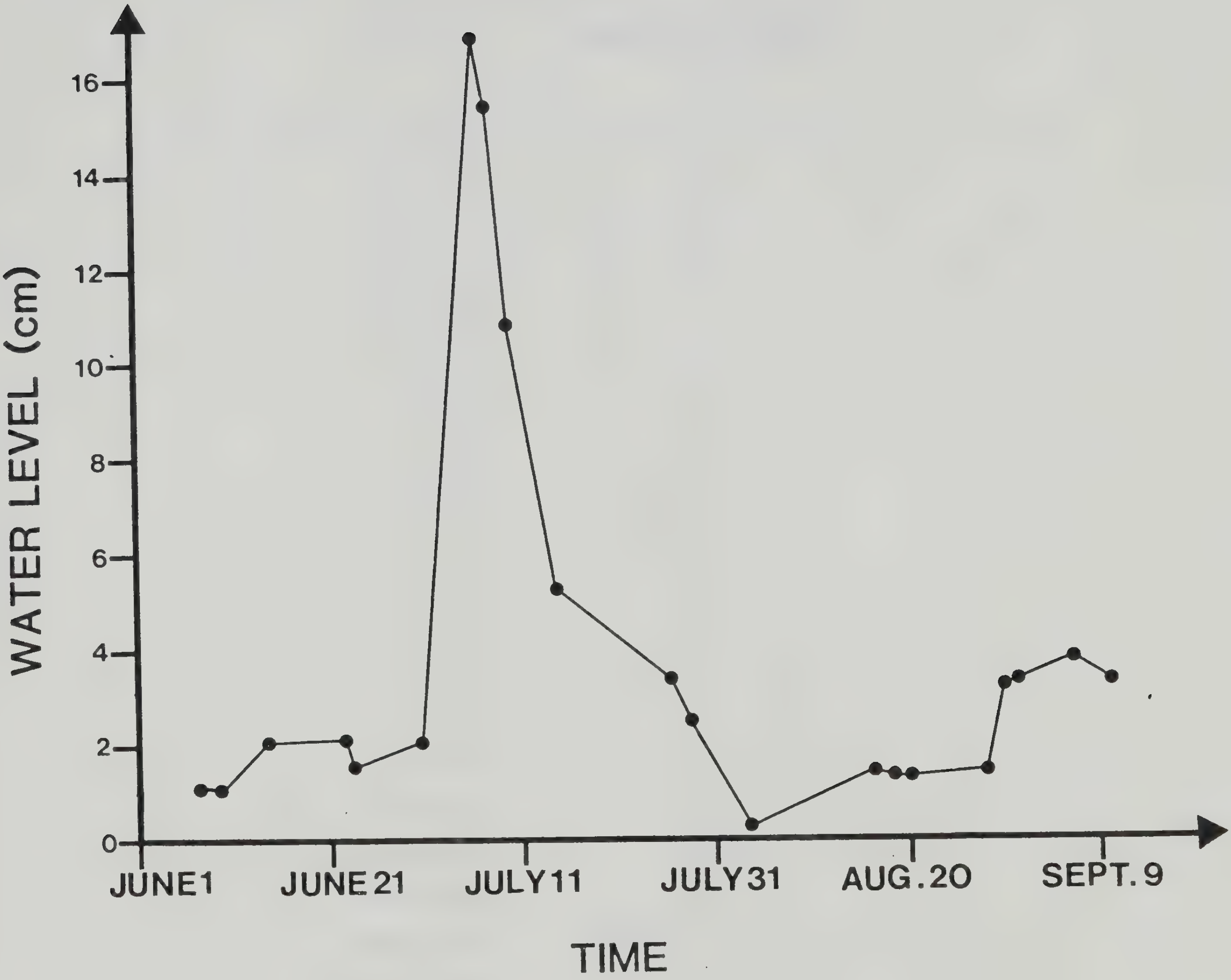
Appendix I: Limnological Data for Roi Lake

Appendix I, Figure 1.

Relative changes in the water level of Roi Lake during the summer months, 1982 (the lowest value was arbitrarily designated as '0').


WATER LEVEL (cm)
0
2
4
6
8
10
12
14
16
JUNE 1
JUNE 21
JULY 11
JULY 31
AUG. 20
SEPT. 9
TIME

Appendix I, Table 1.

Secchi disk readings in Roi Lake, summer months, 1982.

DATE	SECCHI DISK READING (metres)
June 7	7.0
June 9	7.0
June 14	5.5
June 16	5.0
June 18	5.3
June 23	5.0
June 24	5.0
June 30	5.0
July 6	4.3
July 9	5.8
July 13	6.4
July 14	6.0
July 28	7.3
July 29	7.5
Aug. 16	7.5
Aug. 18	8.0
Aug. 20	8.0
Aug. 28	7.5
Aug. 30	7.5
Aug. 31	7.5
Sept. 6	7.3

Appendix I, Table 2.

Temperature profiles at Stations I-IV, Roi Lake, summer months, 1982.

		WATER TEMPERATURE (DEGREES CELSIUS)			
DATE	DEPTH	STATION I	STATION II	STATION III	STATION IV
June 3	0	16.1	16.3	16.1	16.6
	1	16.0	16.0	15.8	16.3
	2	15.8	15.4	15.6	16.0
	3	14.0	14.4	13.9	14.1
	4	10.8	10.8	10.9	11.0
	5	8.1	8.2	8.0	8.1
	6	7.5	6.9	7.0	7.1
	7	****	6.2	6.2	6.7
	8	****	5.8	5.5	****
	9	****	****	5.2	****
	10	****	****	5.0	****
	11	****	****	5.0	****
	12	****	****	5.0	****
	13	****	****	5.0	****
	14	****	****	5.0	****
	15	****	****	5.0	****
	16	****	****	5.0	****
	17	****	****	5.0	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)			
DATE	DEPTH	STATION I	STATION II	STATION III	STATION IV
June 7	0	14.6	14.7	14.7	14.7
	1	14.7	14.7	14.7	14.7
	2	14.7	14.6	14.7	14.7
	3	14.4	14.5	11.7	14.5
	4	11.1	11.9	8.4	11.6
	5	8.5	8.4	7.3	9.4
	6	8.3	7.4	6.4	7.5
	7	****	6.4	5.8	7.2
	8	****	5.9	5.4	****
	9	****	5.4	5.1	****
	10	****	5.5	5.0	****
	11	****	****	5.0	****
	12	****	****	5.0	****
	13	****	****	5.1	****
	14	****	****	5.1	****
	15	****	****	5.2	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)			
DATE	DEPTH	STATION I	STATION II	STATION III	STATION IV
June 14	0	20.3	20.2	20.1	20.5
	1	19.7	20.1	19.9	20.1
	2	18.6	18.8	18.5	18.4
	3	16.9	16.6	16.7	16.6
	4	13.6	14.1	13.6	13.2
	5	10.0	10.1	9.7	9.9
	6	8.2	8.4	8.1	8.1
	7	7.1	7.9	7.0	7.8
	8	6.3	****	6.2	****
	9	****	****	5.7	****
	10	****	****	5.3	****
	11	****	****	5.1	****
	12	****	****	5.2	****
	13	****	****	5.2	****
	14	****	****	5.2	****
	15	****	****	5.2	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)			
DATE	DEPTH	STATION I	STATION II	STATION III	STATION IV
June 21	0	21.7	21.6	21.6	21.7
	1	21.7	21.7	21.6	21.6
	2	21.5	21.7	21.5	21.6
	3	18.9	19.1	18.3	18.7
	4	14.5	14.6	14.5	14.4
	5	10.6	11.3	10.3	10.2
	6	8.6	8.8	8.7	8.4
	7	7.7	8.1	7.5	7.4
	8	6.7	8.2	6.6	****
	9	6.1	****	5.9	****
	10	5.3	****	5.5	****
	11	5.3	****	5.3	****
	12	****	****	5.2	****
	13	****	****	5.2	****
	14	****	****	5.2	****
	15	****	****	5.3	****
	16	****	****	5.2	****
	17	****	****	5.3	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)			
DATE	DEPTH	STATION I	STATION II	STATION III	STATION IV
June 29	0	19.5	19.6	19.4	19.6
	1	19.5	19.6	19.4	19.5
	2	19.4	19.5	19.4	19.5
	3	19.4	18.7	19.3	15.2
	4	15.0	15.0	15.2	11.1
	5	11.1	11.6	11.2	9.1
	6	9.0	11.2	8.8	****
	7	7.7	****	7.5	****
	8	****	****	6.5	****
	9	****	****	5.8	****
	10	****	****	5.3	****
	11	****	****	5.1	****
	12	****	****	5.1	****
	13	****	****	5.2	****
	14	****	****	5.2	****
	15	****	****	5.2	****
	16	****	****	5.4	****
	17	****	****	5.4	****
	18	****	****	5.4	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)			
DATE	DEPTH	STATION I	STATION II	STATION III	STATION IV
July 7	0	18.6	18.9	18.6	19.0
	1	18.6	18.6	18.6	18.7
	2	18.6	18.1	18.4	18.3
	3	17.9	17.8	17.8	17.9
	4	17.0	17.1	16.9	16.9
	5	12.2	12.5	12.3	12.8
	6	9.6	11.1	9.3	9.7
	7	8.0	****	7.7	****
	8	****	****	6.9	****
	9	****	****	6.1	****
	10	****	****	5.5	****
	11	****	****	5.2	****
	12	****	****	5.1	****
	13	****	****	5.1	****
	14	****	****	5.1	****
	15	****	****	5.1	****
	16	****	****	5.1	****
	17	****	****	5.2	****
	18	****	****	5.2	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)			
DATE	DEPTH	STATION I	STATION II	STATION III	STATION IV
July 15	0	20.3	20.4	20.1	20.4
	1	20.0	20.1	19.9	20.0
	2	20.0	19.9	19.8	19.9
	3	19.7	19.5	19.7	19.8
	4	17.9	17.3	17.3	17.4
	5	13.4	13.5	13.1	13.3
	6	9.8	10.0	9.6	11.8
	7	8.3	****	7.8	****
	8	****	****	6.8	****
	9	****	****	6.0	****
	10	****	****	5.5	****
	11	****	****	5.2	****
	12	****	****	5.1	****
	13	****	****	5.1	****
	14	****	****	5.1	****
	15	****	****	5.2	****
	16	****	****	5.2	****
	17	****	****	5.2	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)			
DATE	DEPTH	STATION I	STATION II	STATION III	STATION IV
July 21	0	19.3	19.2	19.3	19.3
	1	19.4	19.3	19.3	19.3
	2	19.3	19.3	19.2	19.3
	3	19.3	19.2	19.2	19.2
	4	18.0	18.6	17.8	18.1
	5	13.9	13.8	13.7	13.9
	6	10.8	****	10.0	****
	7	8.2	****	7.9	****
	8	****	****	6.7	****
	9	****	****	6.0	****
	10	****	****	5.5	****
	11	****	****	5.3	****
	12	****	****	5.2	****
	13	****	****	5.2	****
	14	****	****	5.2	****
	15	****	****	5.2	****
	16	****	****	5.3	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)			
DATE	DEPTH	STATION I	STATION II	STATION III	STATION IV
July 28	0	20.6	20.7	20.4	20.8
	1	20.5	20.5	20.3	20.5
	2	20.4	20.4	20.3	20.4
	3	19.9	19.4	19.8	19.9
	4	19.0	18.7	18.6	18.7
	5	14.7	14.9	14.3	14.8
	6	11.3	****	11.2	11.5
	7	8.9	****	8.4	****
	8	****	****	6.8	****
	9	****	****	6.2	****
	10	****	****	5.6	****
	11	****	****	5.3	****
	12	****	****	5.2	****
	13	****	****	5.1	****
	14	****	****	5.1	****
	15	****	****	5.1	****
	16	****	****	5.2	****
	17	****	****	5.2	****
	18	****	****	5.2	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)			
DATE	DEPTH	STATION I	STATION II	STATION III	STATION IV
Aug. 2	0	21.2	21.2	18.4	21.2
	1	21.3	21.2	18.4	21.2
	2	21.2	21.2	18.3	21.2
	3	20.9	20.9	18.3	21.0
	4	19.0	19.2	18.3	19.2
	5	14.8	15.3	17.5	15.8
	6	11.0	****	13.4	****
	7	9.0	****	11.1	****
	8	7.1	****	7.7	****
	9	****	****	6.4	****
	10	****	****	5.6	****
	11	****	****	5.3	****
	12	****	****	5.2	****
	13	****	****	5.2	****
	14	****	****	5.2	****
	15	****	****	5.2	****
	16	****	****	5.2	****
	17	****	****	5.2	****
	18	****	****	5.2	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)			
DATE	DEPTH	STATION I	STATION II	STATION III	STATION IV
Aug. 16	0	18.4	18.7	17.9	18.0
	1	18.4	18.7	17.8	17.9
	2	18.4	18.2	17.8	17.8
	3	18.3	18.2	17.6	17.7
	4	18.3	18.1	17.4	17.6
	5	17.1	18.1	17.3	17.2
	6	13.6	****	14.0	14.2
	7	10.4	****	10.6	****
	8	7.7	****	7.8	****
	9	7.3	****	6.3	****
	10	****	****	5.6	****
	11	****	****	5.3	****
	12	****	****	5.2	****
	13	****	****	5.2	****
	14	****	****	5.2	****
	15	****	****	5.2	****
	16	****	****	5.2	****
	17	****	****	5.2	****

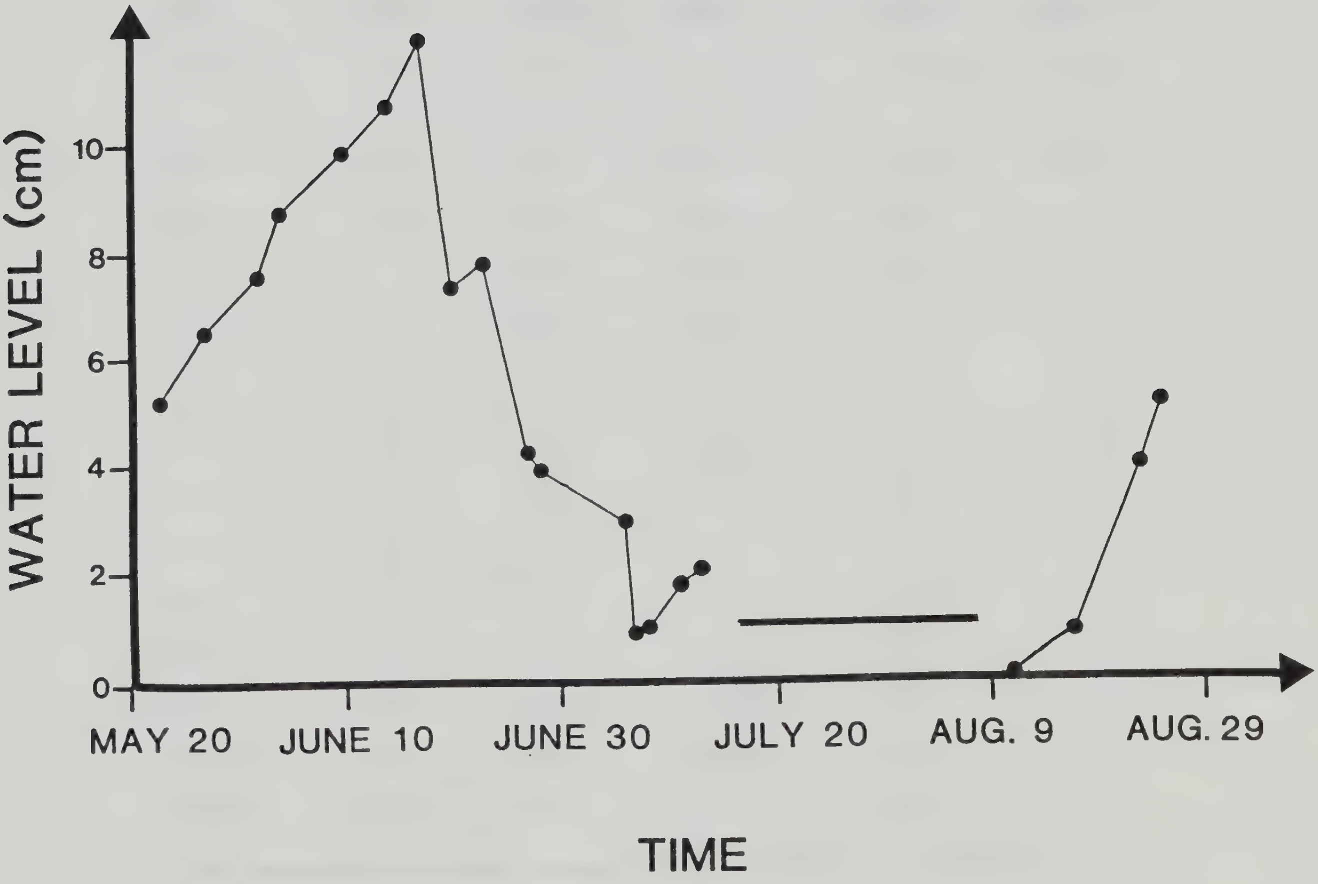
(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)			
DATE	DEPTH	STATION I	STATION II	STATION III	STATION IV
Sept. 15	0	14.3	14.7	14.2	14.6
	1	13.8	14.7	14.1	14.0
	2	13.9	14.0	13.8	13.9
	3	13.8	13.9	13.7	13.9
	4	13.8	13.9	13.7	13.8
	5	13.7	13.8	13.6	13.9
	6	13.7	13.5	13.6	****
	7	12.6	13.5	11.9	****
	8	9.2	****	8.4	****
	9	****	****	6.5	****
	10	****	****	5.7	****
	11	****	****	5.4	****
	12	****	****	5.2	****
	13	****	****	5.2	****
	14	****	****	5.2	****
	15	****	****	5.2	****
	16	****	****	5.2	****
	17	****	****	5.2	****

Appendix II: Limnological Data for Mere Lake

Appendix II, Figure 1.

Relative changes in the water level of Mere Lake during the summer months, 1983 (the lowest value was arbitrarily designated as '0'). The horizontal bar represents a period during which the water level meter was under repair.


WATER LEVEL (cm)
0
2
4
6
8
10
MAY 20
JUNE 10
JUNE 30
JULY 20
AUG. 9
AUG. 29
TIME

Appendix II, Table 1.

Secchi disk readings in Basins I-V, Mere Lake, summer months, 1983.

	SECCHI DISK READING (metres)				
DATE	BASIN I	BASIN II	BASIN III	BASIN IV	BASIN V
May 14	2.6	2.7	3.6	3.2	3.0
May 17	2.6	2.7	3.6	3.2	3.0
May 21	3.0	2.5	2.5	2.2	3.0
May 28	2.1	2.2	2.1	2.1	2.1
June 2	2.0	2.5	2.4	2.2	2.1
June 9	3.0	3.0	3.0	***	3.5
June 22	5.0	4.5	3.5	3.5	5.0
July 11	4.0	4.0	4.0	3.5	4.0
July 19	3.5	4.0	3.5	3.5	4.0
July 25	4.0	4.0	4.0	3.5	4.0
Aug. 2	5.0	4.5	4.5	4.2	4.3
Aug. 13	5.0	4.5	4.5	4.2	4.3
Aug. 22	4.5	4.5	4.2	4.5	4.2

Appendix II, Table 2.

Temperature profiles in Basins I-V, Mere Lake, summer months, 1983.

		WATER TEMPERATURE (DEGREES CELSIUS)				
DATE	DEPTH	BASIN I	BASIN II	BASIN III	BASIN IV	BASIN V
May 14	0	10.4	11.3	11.2	11.1	10.9
	1	10.2	11.0	10.9	10.9	10.8
	2	9.9	10.2	10.6	10.3	10.7
	3	9.7	10.1	9.7	9.9	10.4
	4	9.5	10.0	7.4	9.1	9.6
	5	9.2	9.4	5.6	6.6	6.6
	6	7.9	6.7	4.4	5.6	5.7
	7	7.2	4.7	4.1	4.7	4.2
	8	6.3	4.4	****	4.3	4.2
	9	5.3	4.3	****	4.1	4.2
	10	4.6	4.3	****	****	4.3
	11	4.1	****	****	****	4.4
	12	4.0	****	****	****	****
	13	4.0	****	****	****	****
	14	3.9	****	****	****	****
	15	3.9	****	****	****	****
	16	3.9	****	****	****	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)				
DATE	DEPTH	BASIN I	BASIN II	BASIN III	BASIN IV	BASIN V
May 21	0	12.6	13.0	13.3	13.7	13.3
	1	12.5	12.8	13.1	13.6	13.3
	2	12.5	12.3	12.5	12.4	12.2
	3	12.4	11.9	11.9	12.2	11.6
	4	12.2	11.5	10.7	8.7	10.2
	5	11.6	10.0	7.6	6.8	7.7
	6	8.4	7.6	6.1	5.0	6.2
	7	7.4	5.1	5.1	4.4	4.8
	8	6.4	4.6	4.5	4.4	4.2
	9	5.8	4.5	4.2	****	4.2
	10	5.0	4.4	****	****	4.3
	11	4.7	4.4	****	****	4.3
	12	4.4	****	****	****	4.4
	13	4.3	****	****	****	****
	14	4.2	****	****	****	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)				
DATE	DEPTH	BASIN I	BASIN II	BASIN III	BASIN IV	BASIN V
May 28	0	18.6	18.3	18.7	18.5	18.2
	1	17.9	18.0	17.7	17.9	18.0
	2	16.6	17.7	15.7	15.8	15.8
	3	13.5	13.5	13.2	13.5	13.4
	4	12.2	12.1	10.4	10.5	11.3
	5	11.3	10.7	8.5	7.4	8.5
	6	9.7	7.6	6.2	5.8	6.3
	7	7.9	6.4	5.0	4.7	5.5
	8	6.9	****	4.5	4.5	4.8
	9	6.0	****	4.4	****	4.5
	10	5.2	****	4.5	****	4.4
	11	4.6	****	4.5	****	****
	12	4.5	****	4.5	****	****
	13	4.3	****	****	****	****
	14	4.2	****	****	****	****
	15	4.2	****	****	****	****
	16	4.2	****	****	****	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)				
DATE	DEPTH	BASIN I	BASIN II	BASIN III	BASIN IV	BASIN V
June 9	0	18.9	19.2	19.3	19.3	19.3
	1	18.7	18.7	18.6	19.1	19.1
	2	18.4	18.0	18.2	18.4	18.3
	3	16.9	15.9	15.9	15.6	15.6
	4	13.7	12.9	11.8	11.5	12.1
	5	10.9	10.9	8.8	8.4	9.4
	6	9.5	7.4	7.0	6.0	7.4
	7	8.1	6.4	5.4	4.8	5.9
	8	7.2	5.6	4.7	4.6	4.8
	9	6.3	5.1	4.5	****	4.6
	10	5.0	4.8	4.6	****	4.5
	11	4.8	4.8	4.6	****	4.4
	12	4.5	****	****	****	****
	13	4.4	****	****	****	****
	14	4.4	****	****	****	****
	15	4.5	****	****	****	****

(Table 2 cont'd)

DATE	DEPTH	BASIN I	BASIN II	BASIN III	BASIN IV	BASIN V
		WATER TEMPERATURE (DEGREES CELSIUS)				
June 22	0	15.6	16.0	16.0	16.2	16.0
	1	15.6	16.0	15.9	16.1	15.8
	2	15.4	15.4	15.8	15.6	15.7
	3	15.2	15.6	15.4	15.3	15.4
	4	15.1	14.8	14.4	14.4	15.1
	5	14.5	13.3	9.5	9.2	11.2
	6	9.9	9.1	7.2	6.5	8.3
	7	8.6	****	5.6	5.2	6.4
	8	7.4	****	4.7	4.7	5.6
	9	6.1	****	4.5	4.6	4.7
	10	5.2	****	4.5	****	4.5
	11	4.7	****	4.5	****	4.4
	12	4.5	****	****	****	4.4
	13	4.5	****	****	****	4.4
	14	4.4	****	****	****	4.4
	15	4.3	****	****	****	****
	16	4.3	****	****	****	****
	17	4.3	****	****	****	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)				
DATE	DEPTH	BASIN I	BASIN II	BASIN III	BASIN IV	BASIN V
July 11	0	20.4	20.7	21.1	21.3	20.9
	1	20.3	20.6	20.6	21.0	20.7
	2	20.0	20.5	20.1	20.0	20.0
	3	19.4	18.9	19.4	18.7	19.2
	4	17.0	16.5	15.3	11.5	15.9
	5	15.4	14.1	12.0	7.5	13.1
	6	13.6	11.1	8.3	5.8	9.2
	7	9.8	8.7	6.3	****	7.3
	8	8.0	6.4	5.0	****	5.3
	9	6.8	****	4.6	****	4.7
	10	6.0	****	4.5	****	4.6
	11	5.2	****	4.5	****	4.5
	12	4.7	****	4.5	****	4.4
	13	4.6	****	****	****	****
	14	4.6	****	****	****	****
	15	4.5	****	****	****	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)				
DATE	DEPTH	BASIN I	BASIN II	BASIN III	BASIN IV	BASIN V
July 20	0	21.6	21.4	21.9	22.9	22.0
	1	20.4	21.4	20.5	20.4	20.6
	2	19.2	19.6	19.1	19.2	19.0
	3	18.4	19.0	18.3	18.6	18.4
	4	17.9	18.5	15.9	16.1	17.6
	5	16.6	15.0	12.2	12.3	14.0
	6	13.6	10.9	9.1	8.3	9.8
	7	10.0	8.0	6.1	6.1	7.7
	8	8.5	6.4	5.0	5.0	6.6
	9	7.0	5.7	4.7	****	5.1
	10	5.8	5.5	4.7	****	4.8
	11	5.0	****	4.6	****	4.6
	12	4.6	****	****	****	4.5
	13	4.7	****	****	****	4.5
	14	4.7	****	****	****	4.5
	15	4.7	****	****	****	****
	16	4.7	****	****	****	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)				
DATE	DEPTH	BASIN I	BASIN II	BASIN III	BASIN IV	BASIN V
Aug.2	0	22.7	22.8	23.1	23.3	23.6
	1	22.5	22.7	22.7	22.9	23.2
	2	22.0	22.1	21.9	21.6	21.9
	3	20.6	20.1	20.4	20.4	21.4
	4	19.4	19.0	18.9	17.8	18.7
	5	18.3	16.6	13.7	13.0	14.9
	6	13.8	12.2	9.5	8.8	10.9
	7	10.8	8.5	7.3	6.1	7.5
	8	8.7	6.5	5.4	5.1	6.2
	9	6.8	5.9	4.7	5.2	5.3
	10	6.0	5.7	4.6	****	****
	11	5.0	5.7	4.6	****	****
	12	4.7	****	****	****	****
	13	4.6	****	****	****	****
	14	4.6	****	****	****	****
	15	4.6	****	****	****	****
	16	4.6	****	****	****	****
	17	4.6	****	****	****	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)				
DATE	DEPTH	BASIN I	BASIN II	BASIN III	BASIN IV	BASIN V
Aug. 13	0	22.0	21.9	22.2	22.3	22.3
	1	22.0	21.9	22.1	22.2	22.3
	2	21.9	21.9	22.0	22.0	22.1
	3	21.8	21.5	21.8	21.7	21.7
	4	21.3	20.0	19.4	19.4	19.9
	5	18.6	16.5	15.1	14.4	15.8
	6	15.0	12.6	10.4	9.8	11.0
	7	11.5	9.0	7.3	6.5	8.0
	8	8.9	6.7	5.6	****	6.0
	9	7.2	6.1	5.0	****	5.2
	10	6.0	****	4.8	****	4.8
	11	5.3	****	4.6	****	4.7
	12	4.8	****	4.6	****	4.6
	13	4.6	****	****	****	4.6
	14	4.6	****	****	****	4.6
	15	4.5	****	****	****	4.6
	16	4.5	****	****	****	****
	17	4.5	****	****	****	****

(Table 2 cont'd)

		WATER TEMPERATURE (DEGREES CELSIUS)				
DATE	DEPTH	BASIN I	BASIN II	BASIN III	BASIN IV	BASIN V
Aug.22	0	19.4	18.9	19.0	19.3	20.5
	1	19.0	18.7	18.7	18.9	19.4
	2	18.9	18.6	18.5	18.8	19.1
	3	18.9	18.4	18.4	18.6	18.8
	4	18.8	18.3	18.3	18.2	18.6
	5	18.5	17.6	15.6	15.0	16.1
	6	15.5	13.0	10.7	10.1	11.6
	7	11.6	9.4	7.6	7.0	8.3
	8	9.0	6.9	5.6	5.5	6.3
	9	7.3	6.5	5.0	****	5.2
	10	5.8	5.8	4.9	****	4.9
	11	5.2	5.7	4.9	****	4.7
	12	4.9	****	4.9	****	4.6
	13	4.7	****	****	****	4.6
	14	4.6	****	****	****	4.5
	15	4.6	****	****	****	****
	16	4.6	****	****	****	****

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